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Environment Canada Environnement Canada

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Journal of the Fisheries Research Board of Canada

Identification of the Constituents of Kraft Pulping Effluent that Are Toxic to Juvenile Coho Salmon (*Oncorhynchus kisutch*)

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Leach, J. M., and A. N. Thakore. 1973. Identification of the constituents of kraft pulping effluent that are toxic to juvenile coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 30: 479–484.

The nonvolatile constituents that are acutely toxic to juvenile coho salmon (*Oncorhynchus kistuch*) have been fully identified in a kraft pulping effluent derived from Douglas fir and western hemlock. Toxicity and material balances were maintained through out a fractionation procedure leading to isolation of the toxic factors.

Over 80% of the toxicity was caused by three resin acid soaps: sodium isopimarate (55%), sodium abietate (22%), and sodium dehydroabietate (5%). The remaining toxicity (18%) was contributed by sodium salts of the unsaturated fatty acids: palmitoleic, oleic, linoleic, and linolenic.

Leach, J. M., and A. N. Thakore. 1973. Identification of the constituents of kraft pulping effluent that are toxic to juvenile coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 30: 479–484.

Nous avons identifié au complet les constituants non volatiles responsables de la toxicité de l'effluent d'usinage de pâte à papier kraft à partir du sapin de Douglas et de la pruche de l'Ouest chez les jeunes saumons coho (*Oncorhynchus kisutch*). Nous avons maintenu l'équilibre entre la toxicité et le matériel au moyen d'un procédé de fractionnement aboutissant à l'isolement des éléments toxiques.

Plus de 80% de la toxicité est causée par trois savons d'acide résinique: isopimarate de sodium (55%), abiétate de sodium (22%), déshydroabiétate de sodium (5%). Les sels de sodium des acides gras non saturés palmitoléique, oléique, linoléique, et linolénique sont responsables de la balance (18%).

Received October 10, 1972

The toxicity of kraft pulp mill wastes towards aquatic animals has been reported extensively, but few studies have identified specific toxic materials. Howard and Walden (1965) concluded that up to 75% of kraft mill effluent toxicity could be caused by *p*H values outside the normal biological range. Volatile sulphides and mercaptans are known to contribute to the toxicity of kraft pulping wastes

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(Van Horn et al. 1950; Haydu et al. 1952). They may be rapidly removed, however, by special treatments, such as air stripping and oxidation prior to effluent discharge.

Even after neutralization and elimination of volatile materials the toxicity of kraft mill effluents is appreciable and is of concern because of the immense volumes discharged. Resin acid soaps were amongst the earliest soluble, nonvolatile compounds shown to be toxic to fish in pulpmill wastes. Ebeling (1931) found that 5 mg/liter resin acids killed perch in 40 hr and Hagman (1936) quoted 2 mg/liter or less as a safe level for fish. Van Horn et al. (1950) cited minimum lethal concentrations for minnows of 1 mg/liter resin acid soaps or 5 mg/liter fatty acid soaps; *Daphnia* and insect larvae were less sensitive. More recently, Mäenpää et al. (1968) found the 4-hr LC50 for *Daphnia pulex* to be 2 mg/liter resin acid sodium salts.

There have been no reports of studies designed to completely account for the toxic components in individual kraft mill waste streams. Warren and Marvell (1961) ascribed 7% of the toxicity of condensate, obtained by evaporation of pulping liquor, to 4-(*p*-tolyl)-1-pentanol. Banks (1969) later produced evidence that an unidentified diol, present in the condensate in miniscule quantities, was also toxic. In the only examination of kraft pulp bleaching wastes, Das et al. (1969) revealed putative tetrachloro-*o*-benzoquinone as a toxic factor in effluent from the chlorination stage.

The objective of the present study was to identify, isolate, and assess the toxic contribution of all the nonvolatile constituents in unbleached whitewater (UWW). This is the major waste stream from the pulping section of a kraft mill and is generated during washing and screening of the wood pulp before it is dried or bleached. Toxicity to juvenile coho salmon (*Oncorhynchus kisutch*) was monitored by bioassays at all stages of a chemical fractionation procedure based on chromatographic techniques.

Materials and Methods

General

Amberlite XAD-2 macroreticular resin (Rohm and Haas Company) was Soxhlet extracted with ether and methanol before use to eliminate soluble, low molecular weight material. Unbleached whitewater was sparged with nitrogen to remove oxygen and volatile constituents prior to passage at 2 C over the resin. Solvents were removed rapidly from separated chemical fractions by evaporation under reduced pressure at temperatures below 40 C to minimize isomerization of unstable species. Dried isolates were stored at −10 C.

Fractions were monitored by gas chromatography (GC) and thin-layer chromatography (TLC). A Perkin-Elmer Model 881 temperature-programmed instrument equipped with a flame ionization detector was used for GC analyses. Two stainless steel columns were employed. Most work was done using Column A, 6 ft × ⅛ inch, which contained 15% DEGS on 60–80 Chromosorb W. Column B, 12 ft × ⅛ inch, was packed with 15% SE 30 on Chromosorb W.

Individual compounds were identified initially by combination GC-mass spectrometry (MS). Eluants from a Varian Associates 1600 Aerograph GC instrument containing a DEGS column were passed directly into a Hitachi Perkin-Elmer RMU-6E mass spectrometer.

Fractionation Procedures

The complete fractionation scheme is outlined in Fig. 1. Discrepancies between the weights of materials used in successive stages of the fractionation are due to requirements for bioassays and other studies of sublethal effects of toxicants to fish.

Unbleached whitewater (850 liters), *p*H 10.4, was collected over 2 hr from a British Columbia coastal bleached-kraft mill that was pulping a mixture of Douglas fir and western hemlock chips. The effluent was filtered to remove pulp fibers and processed continuously over an 84-hr period through columns containing Amberlite XAD-2 resin. Aliquots of the eluate from the columns were tested for toxicity at regular intervals. Material adsorbed on the resin was removed by washing with diethyl ether followed by methanol. The residue left on evaporation of ether was dried in vacuo over KOH to give a toxic, dark brown gum (61.83 g). The methanol fraction was not toxic and was not examined further.

The ether extract (59.36 g) was chromatographed on a column of silica gel (J. T. Baker Reagent). Successive elutions with petroleum ether and methanol gave a colorless, nontoxic oil (32.13 g) and a toxic semicrystalline brown oil (26.68 g), respectively. Gas chromatographic and TLC analysis of the brown oil, after methylation with diazomethane, indicated the presence of fatty acids and resin acids.

Selective esterification of fatty acids in the brown oil (22.14 g) using the method of Sheers and Stevenson (1960) was carried out at room temperature for 16 hr to avoid isomerization of labile constituents. Because of steric hindrance resin acids did not react and were extracted from the mixture of fatty acid methyl esters with dilute NaOH. Acidification of the caustic solution, followed by ether extraction, yielded free resin acids (13.68 g). Fatty acid esters were saponified with 40% NaOH and the free fatty acids (8.29 g) recovered in a similar way.

The resin acid fraction (4.03 g) was decolorized by chromatography on silica gel. Resin acids (2.73 g) were eluted gradually in chloroform followed by colored components (0.92 g) in methanol. The resin acids (1.00 g) were fractionated on a column of silica gel impregnated with 25% silver nitrate (Adsorbosil CABN; Applied Science Laboratories Inc.) by a modification of the technique of Norin and Westfelt (1963). Slow elution with

chloroform gave a mixture of abietic-type acids (0.56 g) followed by a mixture of pimaric-type acids (0.44 g). The two fractions were chromatographed again using gradient elution from 50/50 petroleum ether–benzene to 100% benzene. Abietic-type acids (0.40 g) were separated into dehydroabietic acid (0.11 g) and abietic acid (0.29 g); pimaric-type acids (0.32 g) were separated into isopimaric acid (0.29 g) and sandaracopimaric acid (0.03 g). Resin acid composition was checked before and after silver nitrate–silica gel chromatography to ensure that no chemical modification had occurred. The identity and purity of each compound was confirmed by comparison of infrared (IR), ultraviolet (UV), ^1H nuclear magnetic resonance (NMR), and mass spectra with data reported by Zinkel et al. (1971) and with spectra obtained for authentic samples.

The fatty acid fraction was methylated with diazomethane and analyzed by GC (Column A, programmed from 50 to 150 C at 12 C/min, N_2 flow 30 ml/min) using behenic acid as an internal standard. The identity of each fatty acid methyl ester was confirmed by combination GC–MS using pure samples (Applied Science Laboratories Inc.) for comparison.

Bioassays

Toxicities of neutralized effluents and isolates were compared in static bioassays at 11 C using underyearling coho salmon (*Oncorhynchus kisutch*) of 1.2-g mean body weight. The volume of bioassay solution was limited by the amount of materials available to 3 liters in the early stages of the separation and later to 6 liters when the fish were larger. Since fish density was higher than has been recommended for static bioassays (Sprague 1969), the results were used for intercomparison only. Median survival times (MST) of ten fish were measured to

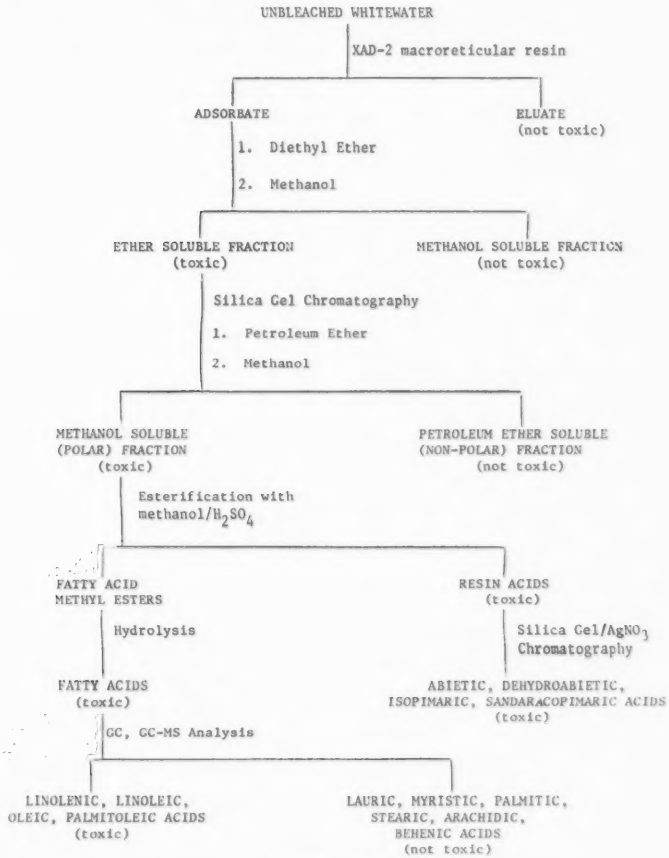

FIG. 1. Fractionation scheme for unbleached whitewater.

a maximum of 96 hr in several concentrations of each solution. Dilutions were made with dechlorinated water (*p*H 6.4, EDTA hardness 6-mg $CaCO_3$/liter) and solutions were aerated sufficiently to maintain dissolved oxygen at saturation level. The normal hyperbolic relation between toxicant concentration and MST was expressed in a linear form using logarithmic plots (Sprague 1969). The log concentration-log MST graph for the original UWW was established using mean MST values from four replicate bioassays at several concentrations of a composite sample that was representative of the effluent processed through XAD-2 resin. To ensure maintenance of a toxicity balance at each stage in the fractionation procedure, individual and recombined fractions were dissolved in alkali, neutralized, and tested by bioassays. Toxic contributions of chemically discrete fractions were found by graphical interpolation (Fig. 2).

Results

All nonvolatile constituents acutely toxic to salmon were identified in the UWW. Material and toxicity balances were maintained throughout the separation procedure.

Resin acid soaps (14.10 mg/liter UWW) were responsible for 82% of the UWW toxicity, whilst the remaining toxic components were sodium salts of unsaturated fatty acids.

Sodium isopimarate, present at a concentration of 5.62 mg/liter in UWW, was the major toxicant and accounted for 55% of UWW toxicity (Fig. 2). A further 22% of the toxicity was caused by sodium abietate (5.73 mg/liter). Sodium dehydroabietate did not cause mortalities when tested at the concentration (2.15 mg/liter) in which it was isolated from UWW, though the typical "cough" response of fish to pulp mill effluents was elicited (Schaumburg et al. 1967). However, since the combined abietate-dehydroabietate fraction was responsible for 27% of UWW toxicity, the dehydroabietate contribution alone was calculated by difference as 5%. A minor component, sodium sandaracopimarate, was found at a concentration of 0.60 mg/liter but did not measurably influence the overall UWW toxicity.

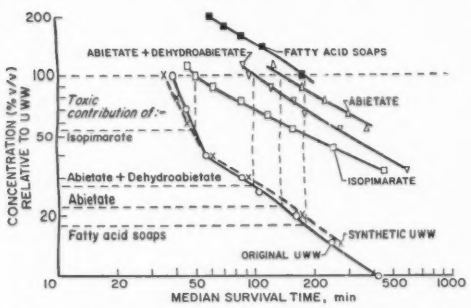

FIG. 2. Bioassay data for unbleached whitewater and isolated toxic fractions.

As confirmation that all resin acid soaps in the UWW had been identified, a synthetic mixture was made at the concentrations found in UWW and was tested by bioassay. Results obtained with the synthetic mixture were identical with those from the isolated resin acid fraction.

Because of the complexity of the fatty acid fraction, individual components could not be isolated quantitatively. Gas chromatographic analysis indicated the presence of at least 24 constituents, the major ones being identified by combination GC–MS. Bioassay data showed that only sodium salts of the unsaturated fatty acids; linoleic (3.57 mg/liter), oleic (1.53 mg/liter), linolenic (1.08 mg/liter), and palmitoleic (1.02 mg/liter); contributed measurably to UWW toxicity. Salts of the saturated fatty acids; lauric (trace), myristic (trace), palmitic (1.89 mg/liter), stearic (1.02 mg/liter), arachidic (0.80 mg/liter), and behenic (trace); were not toxic to salmon at the concentrations found, nor when tested individually at 20 mg/liter. A synthetic mixture of the sodium salts of toxic, unsaturated acids at the correct concentrations in water had toxicity–concentration characteristics identical to the fatty acid fraction isolated from UWW. There was a rapid decline in the toxicity of fatty acid soaps when diluted below their concentration in 100% UWW; at 90% concentration, fish were distressed and disoriented, but were not killed.

Trace quantities of methyl isopimarate and methyl abietate were detected by GC in the fatty acid fraction. They were subsequently shown by analysis to be present in the ether extract of XAD-2 resin, indicating their existence in the original UWW effluent. The methyl esters were, however, not toxic even when tested in amounts equivalent to the UWW concentration of resin acid soaps. The acute toxicity of free resin acids was also much less than that of the sodium salts. For instance, when tested at 100% UWW concentration in the free acid form, the resin acid fraction isolated from UWW gave a MST of 234 min, compared with a MST of 40 min for the sodium salt form. At 80% UWW concentration, the free acids were not toxic, whereas the sodium salts killed 50% of exposed fish in 47 min.

As a final demonstration that *all* the toxic factors in the UWW were accounted for, a solution was made up containing the resin acid fraction plus individual, unsaturated fatty acids at the concentrations found in UWW. Bioassay results were within 2% of those obtained in the original effluent (Fig. 2).

Figure 3 shows the relative toxicities of various resin and fatty acid sodium salts. For isopimarate,

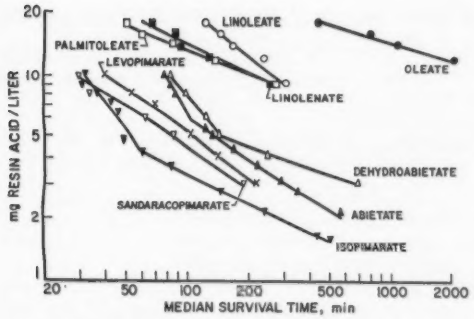

FIG. 3. Bioassay data for various resin acid and fatty acid sodium salts.

no mortality occurred at 1 mg/liter; for all other acids shown, fish survived in solutions containing 1 mg/liter less than the lowest concentration plotted. Under the test conditions, therefore, lethal threshold concentrations for resin acid soaps were between 1 and 3 mg/liter, and lethal thresholds for fatty acid soaps (except oleic) were between 8 and 9 mg/liter. The data are for intercomparison only since the static bioassay conditions used could permit some detoxification.

Discussion

The toxic factors in kraft pulping effluent (UWW) generated from 50% Douglas fir, 50% western hemlock were completely accounted for at all stages of the fractionation procedure by matching the log concentration-log MST graphs of isolated and recombined fractions with the bioassay data obtained for UWW (Fig. 2). The risk of undetected losses of toxicants was thus minimized. That the final toxicity balance so closely approximated 100% was, perhaps, fortuitous in view of the error inherent in measuring MST values of short duration. Nonetheless, this is strong evidence that no toxicant of significance has been overlooked. Fractions designated not toxic (Fig. 1) did not kill fish even when tested at concentrations 2–4 times those found in the UWW. A considerable increase in the levels of constituents in the nontoxic fractions, relative to the toxic resin and fatty acid fractions, would be necessary, therefore, for other chemical compounds to become important contributors to kraft pulping effluent toxicity.

There was a rapid decline in the contribution of the fatty acid fraction to UWW toxicity as concentration decreased. The four unsaturated fatty acid sodium salts responsible for the toxicity of this fraction gave an MST of 170 min when tested at 6.20 mg/liter, the concentration at which they were found in UWW. However, at 90% of this level there were no fish mortalities. Thus, only 10% (0.62 mg/liter) reduction in the concentration of the unsaturated fatty acid constituents would eliminate the toxic influence of the fatty acid fraction and result in almost 20% decrease in UWW toxicity.

The wide variations in effluent toxicity often observed within and between mills may be the result of quite small deviations in toxicant concentrations. Differences in the concentration of the wood extractives responsible for UWW toxicity might be expected with changes in wood species (Assarsson and Åkerlund 1966), the preponderance of heartwood or sapwood (Hancock and Swan 1965), or the age of wood chips used in the pulping process. There may not be, however, a simple correlation between the resin and fatty acid composition in wood chips and their concentrations in UWW because of isomerization and other reactions that may occur during pulping.

The resin acid concentration of 13.06 mg/liter UWW reported here may be compared with the value of 2.6 mg/liter found by Mäenpää et al. (1968) for a similar effluent from a Finnish mill producing pine kraft pulp. Using GC analysis, Mäenpää et al. identified abietate and dehydroabietate as the main resin acid soap constituents. They also found small amounts of pimarate, palustrate, and neoabietate, but did not detect isopimarate, the major toxicant isolated in the present study. Whilst developing the fractionation scheme, one batch of UWW appeared to contain traces of neoabietate and either levopimarate or palustrate. The thermodynamic instability of these compounds precludes their survival in substantial quantities at the pulping temperature of 170 C.

The compound 4-(p-tolyl)-1-pentanol was not found in the UWW, though it has previously been identified (Warren and Marvell 1961) as a toxic constituent of evaporator condensate from a west coast softwood kraft mill. Both UWW and evaporator condensate are derived from pulping liquor.

There has been no published information on the toxicity of individual resin and fatty acid soaps towards salmonids. The results of static bioassays, shown in Fig. 3, illustrate the relative toxicities of selected resin and fatty acid soaps and give an indication of lethal threshold concentrations. Pimaric-type acids were more toxic than abietic-type acids. The toxicity of C_{18} fatty acid sodium salts decreased with diminishing degree of unsaturation in the order linolenate, linoleate, and oleate. Palmitoleate, a C_{16} mono-unsaturated acid, was the most toxic fatty acid soap tested. Experiments to measure incipient LC50 values for all these com-

pounds are underway using flow-through bioassay techniques.

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Temperature Effects on Mercury Accumulation, Toxicity, and Metabolic Rate in Rainbow Trout (*Salmo gairdneri*)

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MacLeod, J. C., and E. Pessah. 1973. Temperature effects on mercury accumulation, toxicity, and metabolic rate in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 485–492.

Mercury toxicity in rainbow trout fingerlings was related to temperature and chemical formulation of the mercury. At 10 C, the 24-hr TL_m concentration (median tolerance limit) for mercuric chloride ($HgCl_2$) was approximately 30 times that for phenyl mercuric acetate (PMA). The 96-hr TL_m values for mercuric chloride at 5, 10, and 20 C were 0.40, 0.28, and 0.22 mg Hg/liter. The velocity of mortality, (V = reciprocal of time to death in hours), was linearly related to temperature. For a mercuric chloride concentration of 0.5 mg Hg/liter, $V = .002 + .0023t$, where t = temperature in centigrade degrees.

Temperature also affected accumulation rate of mercury in the fish muscle. At 5, 10, and 20 C a mercuric chloride concentration of 0.1 mg Hg/liter in the water produced biological magnification factors (conc. in fish ÷ conc. in water) of 4, 10, and 22×, respectively. PMA produced higher magnification factors of 80–100× at 10 C.

Active metabolic rate, though increased by higher temperatures, was depressed by mercuric chloride, and higher temperatures augmented the depressant effect.

MacLeod, J. C., and E. Pessah. 1973. Temperature effects on mercury accumulation, toxicity, and metabolic rate in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 485–492.

La toxicité du mercure chez des alevins de truite arc-en-ciel est liée à la température et à la formule chimique du mercure. La concentration de TL_m (limite de tolérance médiane) après 24 h pour le chlorure mercurique ($HgCl_2$) est d'environ 30 fois celle du phénylmercuracétate (PMA). Les valeurs de TL_m après 96 h pour le chlorure mercurique à 5, 10, et 20 C sont de 0.40, 0.28, et 0.22-mg Hg/litre. La vélocité de mortalité (V = l'inverse du temps à mourir en heures) est en relation linéaire avec la température. A une concentration en chlorure mercurique de 0.5-mg Hg/litre, $V = .002 + .0023t$, où t = température en degrés centigrades.

La température affecte également le taux d'accumulation du mercure dans le muscle du poisson. A 5, 10, et 20 C, une teneur en chlorure mercurique de 0.1-mg Hg/litre dans l'eau produit des facteurs d'amplification biologique (concentration dans le poisson ÷ concentration dans l'eau) de 4, 10, et 22×, respectivement. Le PMA produit des facteurs d'amplification plus élevés, soit 80–100× à 10 C.

Des températures élevées causent une augmentation du taux de métabolisme actif, alors que le chlorure mercurique produit un abaissement. Cependant, l'interaction est telle que les températures élevées accentuent l'effet déprimant du mercure.

Received April 7, 1972

This study is part of a program at the Freshwater Institute investigating the effects of mercury contamination in fish and aquatic ecosystems. First reports of significant concentrations of mercury in Canadian fish were from the Saskatchewan River system (Wobeser et al. 1970), and since then contamination has been uncovered in other parts of Canada (eg. Bligh 1970, 1971; Uthe and Bligh 1971; Fimreite 1970).

In the present study inorganic mercury in the form of mercuric chloride $HgCl_2$, and organic mercury in the form of PMA (phenyl mercuric acetate, $C_6H_5HgCOOCH_3$), were tested for their effects on rainbow trout at different temperatures. Mercuric chloride is found in effluents from some chlor-alkali plants which are listed as major industrial pollution sources of mercury in Canada (Fimreite 1970). PMA has been widely used as a slimicide in pulp mills.

Temperature is the most important environmental factor controlling rates of biological processes and thus would be expected to influence tissue uptake of mercury and toxicity tolerance in fish. Fish are known to contain more mercury and to

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be less tolerant to mercury in the water at warmer temperatures (Hasselrot 1968; Amend et al. 1969; Boëtius 1960). Little else is known about the interacting effects of temperature and mercury on fish, or to what degree concentrations of mercurial compounds in water affect the respiratory metabolism or swimming performance in fishes. The specific objectives of the present study were to determine the effects of temperature on: mercury toxicity, residue accumulation in the edible or "dressed" portion of the fish, and active metabolic rate of fish exposed to mercury.

Materials and Methods

Experimental Animals and Water Supply

Hatchery reared rainbow trout fingerlings from the same lot and ranging in weight from 9 to 28 g were held for at least 2 months in the laboratory at the various test temperatures ± 1 C. They were fed dry trout food pellets and no prophylactic treatments were applied to the fish in the course of the study. All tests were conducted in dechlorinated city tap water which had the following chemical constituents (in mg per liter):

Calcium (Ca)	–	27.2
Magnesium (Mg)	–	5.8
Sodium (Na)	–	1.9
Iron (Fe)	–	.05
Chloride (Cl)	–	1.5–5.5
Sulphate (SO_4)	–	15.0
Fluoride (F)	–	0.95
Total hardness ($CaCO_3$)	–	90
Total solids	–	130
Suspended solids	–	10

*p*H was 7.5 to 7.8

Acute Toxicity tests

A proportional dilution apparatus (Mount and Brungs 1967) delivered five concentrations of toxicant at each of three temperatures (Table 1) to 30-liter glass aquaria each of which held 16 to 21 fish. Time to 95% replacement of the test solution was 6 hr as determined from Sprague (1969). Temperature was controlled to ±0.3 C. As reliable measurements of mercury levels in test aquaria were not available at the time, KNO_3 was used to calibrate the apparatus. Determinations on aquaria inflows over a 3-day period showed an average coefficient of variation of 5.3%.

Each aquaria was divided into two compartments, one holding 10 to 15 fish for assessing mortality and the other six fish for mercury residue determinations in their flesh. Probit plots of cumulative percentage mortality vs. time to death were used to calculate the TD50 (time to death of 50% of the individuals). The 95% confidence intervals were determined by Litchfield's (1949) method. Linear toxicity curves were obtained using a hyperbolic plot of the reciprocal of the TD50 against concentration of mercury in the water. These plots were used to estimate the 96 hr TL_m values (50% tolerance limit or the concentration in which 50% of the fish survived for 96 hr).

Velocity of mortality (V) was defined as the reciprocal of the TD50 (median time to death in hours). Linear regression equations of the relation between V and temperature were calculated for mercuric chloride concentrations of 0.5 and 1.0 mg Hg/liter. These concentrations were selected because at least 50% of the fish died in these concentrations — a necessary requirement to measure the TD50. Q_{10} values were calculated for velocities of mortality at different temperatures after the formula given by Hoar (1966).

Mercury Residues

Two fish were removed from each aquarium after 6, 24, and 96 hr of exposure. Fish for all residue analyses were frozen whole and later thawed and weighed. The

TABLE 1. Comparison of active metabolic rates (mg O_2/kg of fish per hour) of salmonid species as determined by various methods and authors.

	Graham (1949)	Job (1955)	Basu (1959)	Gibson and Fry (1954)	Brett (1964)	Dickson and Kramer (1971)	Present study
Temp. (C)	*S. fontinalis* (16–62)[a] A[b]	*S. fontinalis* (10–30) A	*S. fontinalis* (164) B	*S. namaycush* (16–38) A	*O. nerka* (50) C	*S. gairdneri* (137–249) D	*S. gairdneri* (10–30) E
5	240	240	–	–	510	380	380
10	350	240	330	300	620	470	440
15	500	320	390	440	880	580	–
20	530	350	330	400	840	570	730

[a]Weight of fish (g).

[b]Respirometer Type: A, Fry and Hart (1948) rotating annular chamber, no electric stimulus; B, Basu, (1959) rotating annular chamber, with electric stimulus; C, Brett (1964) tunnel respirometer, with electric stimulus; D, Dickson and Kramer (1971) "Blaska" tunnel respirometer, with electric stimulus; E, Present study — flask with magnetic stirrer, no electric stimulus.

head, fins, and internal organs, including the kidney, were removed. The remaining muscle, bones, and skin were ground to a very fine homogeneous mixture using a small grinding mill.[1] Analyses for total mercury in the fish flesh were done by a wet digestion and flameless atomic absorption spectrophotometric method as described by Armstrong and Uthe (1971).

Standard deviation of this method for single determinations on each sample is 8% or less, depending upon the mercury concentration. In this study three determinations were made on each sample reducing the analytical standard deviation to 4.6% or less.

All survivors of the 96-hr exposure were transferred to aquaria supplied with a continuous flow of temperature-controlled water. These fish were sampled periodically over a 3–6-week period to measure residue levels and to determine elimination rate of mercury from their flesh.

Active Metabolism

Active metabolism determinations were made in respirometer flasks equipped with magnetic stirrers. Tests were of 15 min duration and all procedures followed those of MacLeod and Smith (1966).

Active metabolism determinations should reflect the oxygen consumption of the fish under conditions of maximum energy expenditure. In recent years the trend in active metabolism respirometry has been towards attaining higher values as apparatus improved. A comparison of active metabolic rates derived by various workers using different apparatus was made (Table 1). The only data used were those from salmonid species where dissolved oxygen or other chemicals in the water were not limiting factors. In magnitude the present metabolism values compare favorably with those made by Dickson and Kramer (1971) on rainbow trout using the Blaska tunnel respirometer which is one of the newer types of respirometers in this class. The present method thus appears capable of providing active metabolic rates which, under the conditions of this study, compare favorably with other techniques. To predict the active metabolic rate at any concentration of mercuric chloride in the water the linear equation $Y = mX + b$, relating metabolism to mercury concentration, was determined for each temperature. These equations were then used to calculate active metabolism values for two selected sublethal mercury concentrations, 0.1

[1]Micro beating mill, Canlab Laboratory Equipment.

TABLE 2. 48 and 96 hr median tolerance limits of mercuric chloride for rainbow trout at three temperatures.

$HgCl_2$ (*mg Hg/liter*)	Av. wt. fish (*g*)	% dead at 96 hr	Time to 50% mortality (*hr*)	TL_m (*mg Hg/liter*)	
				48 hr	96 hr
		5 C			
0.00	15.5	0.0	–		
0.10	11.2	0.0	–		
0.25	10.8	0.0	–		
0.49	9.5	93.4	77.5(73.2–83.8)[b]	0.65	0.40
0.95	9.1	100.0	26.5(23.7–30.0)		
2.00	15.3	100.0	12.0(10.9–13.2)		
		10 C			
0.00	19.6	0.0	–		
0.07	18.8	0.0	–		
0.19	21.3	0.0	–	0.45	0.28
0.37	15.2	100.0	51.7(47.0–56.8)		
0.71	19.1	100.0	26.7(23.9–29.7)		
1.50	13.2	100.0	10.3(8.3–12.9)		
		20 C[a]			
0.00	23.1	0.0	–		
0.05	27.8	0.0	–		
0.12	20.0	10.0	–	0.30	0.22
0.24	24.9	10.0	–		
0.48	23.2	60.0	23.3(18.5–29.4)		
1.00	18.5	100.0	9.0(7.3–11.1)		

[a]Ten fish in each test, 15 in tests at 5 and 10 C.
[b]95% confidence limits.

and 0.2 mg Hg/liter, at 5, 10, and 20 C. Curves were then constructed describing the combined effect of temperature and mercury concentration upon active metabolism.

Temperature Effects on Acute Toxicity of Mercury

Visible signs of poisoning included loss of equilibrium, frequent surfacing and sinking, and periodic bursts of erratic swimming. A darkening in coloration and a gradual onset of inactivity preceded death. Fish did not exhibit symptoms of anoxia or have flared gill chambers, as typically occurs in acute poisoning from some other heavy metals such as copper. The gills in moribund fish appeared normal under low magnification.

Toxicity curves gave estimated 96-hr TL_m values of 0.40, 0.28, and 0.22 mg Hg/liter at 5, 10, and

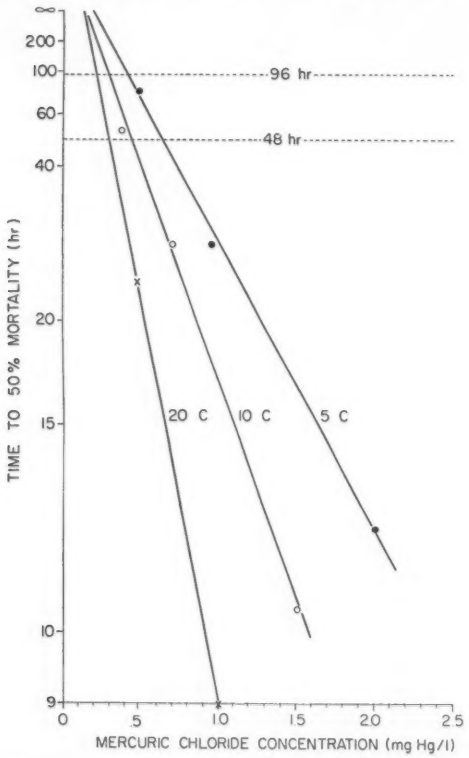

FIG. 1. Toxicity curves for rainbow trout exposed to various concentrations of mercuric chloride at 5, 10, and 20 C for 96 hr. Vertical axis is on a hyperbolic (reciprocal) scale.

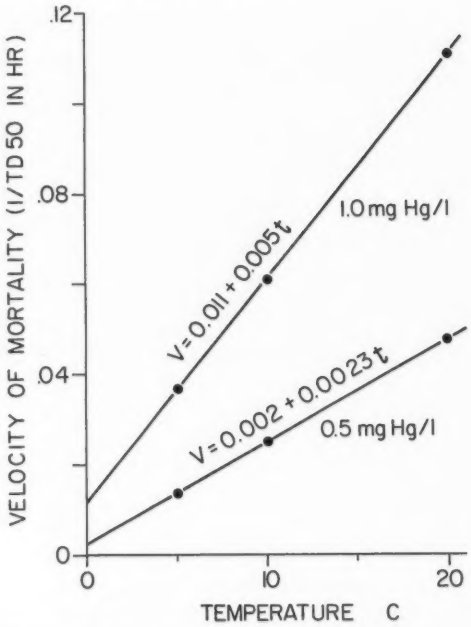

FIG. 2. Relation of velocity of mortality to temperature for concentrations of mercuric chloride of 0.5 and 1.0 mg Hg/liter. Data points are derived from the toxicity curves in Fig. 1.

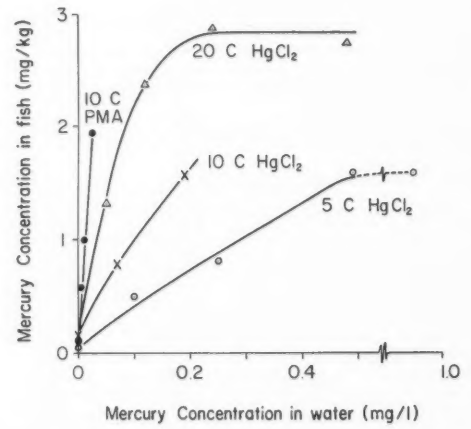

FIG. 3. Mercury concentrations in muscle tissue of rainbow trout exposed for 4 days to various concentrations of mercuric chloride and PMA at different temperatures. (Data for PMA is interpolated from measurements made after 7 days exposure.)

20 C, respectively (Table 2, Fig. 1). A more precise definition of the relation between toxicity and temperature may be described by the linear equation

$$V = a + bt$$

where, V = velocity of mortality $= \frac{1}{TD50}$

$TD50$ = time to death, in hours, of 50% of the fish

t = temperature in C

a = intercept on vertical axis

b = slope.

Velocity of mortality plots against temperature at the two concentrations tested (Fig. 2) showed that increased temperature greatly increased the toxicity of mercuric chloride. The slope for 1.0 mg Hg/liter was greater than for 0.5 mg Hg/liter indicating that temperature has a greater effect on modifying the toxicity when mercury levels in the water are higher.

The Q_{10} values for velocity of mortality from two concentrations of mercury at three temperature ranges were:

Temp. range	0.5 mg Hg/liter	1.0 mg Hg/liter
5–10 C	3.2	2.9
10–15 C	2.0	2.0
15–20 C	1.7	1.7

The Q_{10} values at 5–10 C were almost double those between 15 and 20 C. This indicates that similar temperature changes have much larger effects on mercury toxicity at lower than at higher temperatures.

TABLE 3. Biological magnification factors (conc. in tissues ÷ conc. in water) for mercury accumulating in trout exposed to different concentrations of $HgCl_2$ and PMA for 4 days at three temperatures.

Conc. in water (*mg Hg/liter*)	Magnification Factor[a]		
	5 C	10 C	20 C
	$HgCl_2$		
0.05	5.0	12.0	26.0
0.10	4.0	10.0	22.0
0.20	3.8	8.5	14.0
	PMA		
0.005	–	100	–
0.010	–	90	–
0.020	–	80	–

[a]For PMA, values were interpolated as exposure period was 7 days.

One TL_m test was performed using PMA at 10 C with 10 fish at each concentration (average weight per fish was 22.9 g). A 24-hr TL_m concentration was established at 0.025 mg Hg/liter as PMA. Interpolating from Fig. 1 the 24-hr TL_m of mercuric chloride is 0.75 mg Hg/liter. PMA thus appears to be some 30 times more toxic than mercuric chloride.

Effects on Accumulation and Elimination of Mercury

Temperature greatly influenced accumulation rate of mercury in the fish flesh (Fig. 3). For example, after 4 days exposure to a mercuric chloride con-

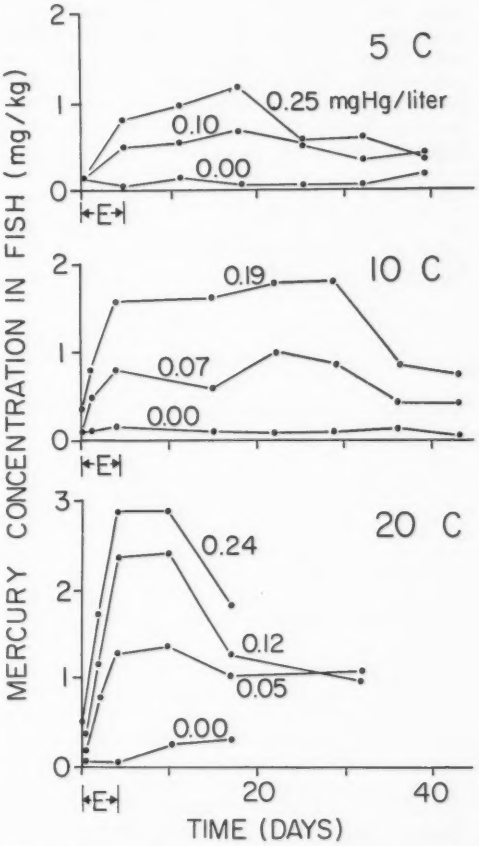

FIG. 4. Mercury concentrations in trout exposed for 96 hr to various concentrations of mercuric chloride and then held up to 45 days in fresh running water at 5, 10, and 20 C. Each point represents a sample of two fish. "E" indicates the 96-hr exposure period.

centration of 0.1 mg Hg/liter in the water the biological magnification factors at 5, 10, and 20 C were calculated as 4, 10, and 22× respectively (Table 3).

Concentration of mercury in the fish flesh was also related to concentration of mercury in the water for both PMA and mercuric chloride (Fig. 3). For example at 5 C, 4 day exposures to 0.1 and 0.5 mg Hg/liter produced concentrations in the flesh of 0.4 and 1.6 mg Hg/kg, respectively. The highest magnification factors occurred at the lowest mercury concentrations in the water, indicating greater uptake efficiency at lower concentrations (Table 3). PMA had much higher biological magnification than did mercuric chloride. A concentration of .005 mg Hg/liter in the water was calculated to produce 0.5 mg Hg/kg in the flesh after 4 days of exposure, giving a magnification of 100×.

Elimination of mercury from the fish flesh was dependent upon temperature. After 40 days in fresh running water, treated fish still retained levels of mercury in the "dressed portion" (Fig. 4). At 5 and 10 C, concentrations in the dressed portion did not decrease until 20–30 days after exposure terminated. However, at 20 C reduction in mercury concentration in the tissue was apparent after 10 days.

Effects on Active Metabolism

Active metabolic rates were directly related to temperature but inversely related to mercury concentrations in the water. The correlation between active metabolism and mercuric chloride in the water was significant at 10 and 20 C but not at 5 C (Table 4). The curves describing the combined effect of temperature and mercury concentration (Fig. 5) indicate a marked interaction of these factors in their effects on active metabolism. At 20 C, it was calculated that 0.1 mg Hg/liter reduced active metabolism from 730 to 658 mg O_2/kg per hour, a reduction of 10%, whereas at 10 C the same mercury concentration produced a depression of only 5%. The interaction appears to be such that

TABLE 4. Active metabolism of rainbow trout after exposure for 96 hr to various concentrations of mercuric chloride at three temperatures. Numerals in parenthesis are numbers of replicates, each based on four fish per respirometer except that three fish were used at 20 C.

Temp.	Mercury conc. (*mg Hg/liter*)	Active metabolism (*mg O_2/kg/hr*)	Avg. fish wt. (*gm*)	O_2 conc. in respirometer (*mg/liter*)	Correlation Coeff. (*r*)	Regression equation
5 C	0.00	383±13[a] (4)	9.3	7.8	−0.46	Y=−123X+395
	0.10	402±13 (4)				
	0.25	356±9 (4)				
10 C	0.00	441±10 (4)	17.2	6.8	−0.61*	Y=−208X+443
	0.07	434±20 (3)				
	0.19	402±12 (3)				
20 C	0.00	726±85 (3)	26.5	7.0	−0.71**	Y=−721X+730
	0.05	645 (2)				
	0.12	708±76 (3)				
	0.24	528±49 (3)				
	0.48	390 (1)				

[a]Mean and one standard error of mean, * = significant at 0.05 level, ** = significant at 0.01 level.

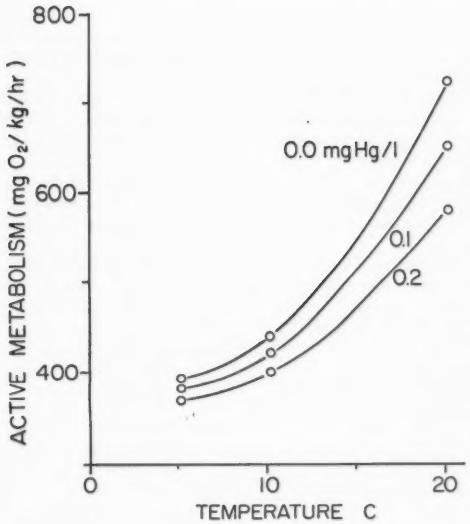

FIG. 5. Effect of temperature on the active metabolism of rainbow trout for two selected concentrations of mercuric chloride. Points are calculated from regression lines in Table 4.

higher temperatures potentiate the depressant action of mercuric chloride.

Discussion

This study suggests that, in nature, seasonal temperature variation could be an important factor influencing the toxicity of mercury in the water. For example, an industry discharging mercuric chloride into a river during the winter might not cause direct fish kills; fish might move through the discharge zone without serious mortality. However during summer conditions when water temperatures rise the velocity of mortality is accelerated. This could result in summer fish kills in an area without any change in pollutant concentration in the water.

The increased toxicity of mercury at higher temperatures is probably related to factors such as rates of chemical reaction, diffusion, active transport of toxic materials across membranes, and metabolic rate. Lloyd (1965) hypothesized that higher metabolic rates increase the rate at which poison reaches the gills which are known to be a major site of uptake for certain toxic chemicals.

The observed depressions in active metabolism in mercury exposed fish at 10 and 20 C are indicative of damage to tissues or a vital system. Fry (1957) demonstrated that depressions in active metabolism directly reduce "scope for activity". This in turn may result in decreased growth, impaired swimming ability and other general debilatory symptoms. It is possible that even a small reduction in the normal active metabolic rate may be indicative of stress in the animals. In the present study a 10% decline in active metabolism was caused by 0.1 mg/liter of Hg in a mercuric chloride solution at 20 C. This concentration is equivalent to 50% of the 96 hr TL_m and some mortality might occur in this concentration (Table 2). This suggests that any measurable pollutant-caused depression of active metabolism is a sign of stress not far from the onset of lethal conditions. Other signs of toxicity such as loss of equilibrium, erratic swimming, and gradual onset of inactivity suggested neurological damage. There was no evidence of heavy mucus coagulation on the gills, as occurs with high concentrations of some other heavy metals, nor were there any signs of asphyxia.

The increased accumulation rate of mercury at high temperatures can be interpreted as resulting directly from effects on metabolic rate and hence the rate at which mercury contaminated water is pumped over the gills. Hasselrot (1968) studying caged fish exposed to mercury in polluted Swedish rivers demonstrated higher mercury levels in the fish flesh in summer than in winter.

The higher accumulation rate of PMA as compared with mercuric chloride is probably related to differences in molecular structure (Hannerz 1968).

The 2–4-week delay, before reductions in mercury content of the dressed portion of the fish were observed, is likely attributable to transference from internal organs to the muscle as described by Rucker and Amend (1969). The rate of transference may be accelerated by warmer temperatures, accounting for the earlier decline in mercury concentration at 20 C.

There exists the practical problem of what important factors influence the reduction of mercury in fish populations once pollution is stopped. The present data suggest that warmer temperatures may directly increase the elimination rate of mercury from the fish muscle. Addition of new tissues by growth can also produce a net decrease in mercury concentration in the flesh. Growth rate in many fish species is also directly related to water temperature. Thus temperature may potentially be one of the most important factors influencing the rate at which mercury levels in fish populations return to normal.

Acknowledgments

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Macrobenthic Ecology of a Sawdust-Bearing Substrate in the Penobscot River Estuary (Maine)[1]

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SHOREY, W. K. 1973. Macrobenthic ecology of a sawdust-bearing substrate in the Penobscot River estuary (Maine). J. Fish. Res. Board Can. 30: 493–497.

The macrobenthos of sawdust-bearing substrates in the Penobscot River estuary (Maine) were sampled bimonthly from January through November 1968. The polychaete *Scolecolepides viridis* and the bivalves *Macoma balthica* and *Mya arenaria* dominated the sandy sediments of the shallow station. *Prionospio malmgreni* and *Corophium volutator* were dominant in the granular substrate of the deeper station. The population of the shallow station (1-m depth, mean low water) was seasonally more stable and had a higher mean monthly bio-index (number of individuals/number of species) than that of the deeper station (6-m depth, mean low water).

SHOREY, W. K. 1973. Macrobenthic ecology of a sawdust-bearing substrate in the Penobscot River estuary (Maine). J. Fish. Res. Board Can. 30: 493–497.

De janvier à la fin de novembre 1968, nous avons prélevé bi-mensuellement des échantillons de macrobenthos de substrats contenant du bran de scie dans l'estuaire de la rivière Penobscot (Maine). Le polychète *Scolecolepides viridis* et les bivalves *Macoma balthica* et *Mya arenaria* sont les espèces dominantes des sédiments sableux de la station peu profonde. *Prionospio malmgreni* et *Corophium volutator* prédominent dans le substrat granuleux de la station profonde. La population de la station peu profonde (1 m au-dessous du niveau de basse mer) présente moins de variations saisonnières et possède un bio-indice (nombre d'individus/nombre d'espèces) mensuel moyen plus élevé que la station profonde (6 m au-dessous du niveau moyen de basse mer).

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PRIOR to this investigation, qualitative surveys of the benthos and associated sediments were made during hydrographic surveys of the Penobscot River estuary by Haefner (1967). In an early study of black duck habitats, Hartman's (1960) attempt to use sawdust concentration as a parameter to characterize mud flats was not successful. In the present study, a method was devised to measure the concentration of sawdust in the sediments. It was conducted to determine the nature and seasonal distribution of macrobenthic fauna inhabiting sawdust-bearing substrates in the Penobscot River estuary (Maine).

Materials and Methods

Two stations (Fig. 1) in the Penobscot River estuary were sampled bimonthly from January through November 1968. Station 1 was shallow (1 m at mean low water [MLW]) and adjacent to an intertidal cove (44°30′16″N, 68°46′20″W) on the southeastern tip of Vernona Island. Station 2, approximately 200 m further offshore in 6 m (MLW) of water, was 1.4 km southwest of the mouth of the Orland River estuary.

Hydrographic data were obtained from samples collected within 2 cm of the bottom of the water column. A Frautschy bottle, modified with a special attachment to allow closure in a horizontal position, was used to collect the samples. The temperature of each water sample was measured to the nearest 0.1 C. Dissolved oxygen was determined by the sodium-azide modification of the Winkler method (American Public Health Association 1960) and salinity by silver nitrate titration (Strickland and Parsons 1960).

Three Ponar grab samples of 0.05 m^2 were taken at each station except in January, when only two samples were collected per station. The combined samples were placed in a plastic bag and thoroughly mixed with 25 ml of 1.0% propylene phenoxetol, which served as a

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relaxant for the organisms. The samples were preserved with formalin upon return to the laboratory.

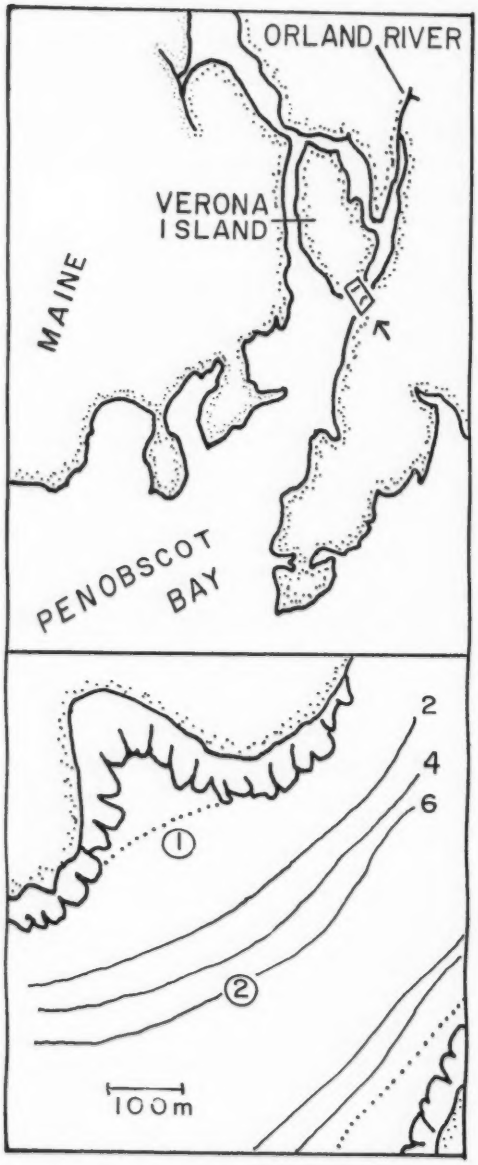

FIG. 1. Maps showing location of Stations 1 and 2 (numbered circles) in the Penobscot River estuary (Maine). Depths in meters (MLW).

Each preserved sample was divided in half. One portion was set aside for later identification and counting of the organisms. The other half was oven-dried at 105 C (Welch 1948) in preparation for texture analysis. The dried sample was then mechanically shaken through sieves 10, 35, 120, and 230 of the U.S. Standard Sieve Series. This separated the sediments into the following fractions: granule ($\geq$ 2.0-mm grain size), coarse sand ($\geq$ 0.5 mm), fine sand ($\geq$ 0.125 mm), very fine sand ($\geq$ 0.063 mm), and silt-clay ($<$ 0.063 mm).

Volumes of the sieve components were measured by displacement in carbon tetrachloride, which permitted the sawdust component to be decanted and removed. The remaining sediment was then suction-dried and its volume measured as before. From these data, the percent composition (by volume) of sediment and sawdust could be calculated per sieve fraction for total volume.

The half-samples to be examined for organisms were wet-sieved through a 0.5-mm mesh screen to remove the finer sediments. The organisms were sorted, identified, and counted, and counts were converted to number of organisms per 0.1 m^2. Polychaeta, Crustacea, and Mollusca were usually identified to species.

The percent composition of each species (or higher taxa) was determined for each month's sample and the mean of the percent composition ($\overline{X}$ %) derived. A weighted mean percent ($\overline{X}_w$ %, based on $\overline{X}$ % multiplied by number of samples in which the particular species was found) was used to rank the organisms in the community. There were 20 and 21 samples from Stations 1 and 2, respectively.

The total number of individuals of each species was obtained and the contribution of each species was calculated as a percent of all specimens collected during the year. This percent contribution was then accumulated ($\sum$ % by no.) for the ranked list of species until 80% of the community was accounted for.

To examine the diversity patterns of the two stations, the bio-index (number of individuals per unit area of 0.1 m^2 / number of species) was calculated for each month. For a general diversity pattern of the stations, a mean of the monthly bio-indices was derived.

Results

Although Stations 1 and 2 were both characteristically polyhaline (18–30‰), salinity was always slightly higher at the deeper station (Fig. 2). Station 1 was markedly affected by spring runoff; in April, its salinity (10.2‰) was much lower than that of Station 2 (19.3‰). Water temperatures of Station 1 were about a degree higher than those of Station 2 throughout the year.

Dissolved oxygen concentrations of the two stations were similar throughout the year (7–13 ppm), usually differing no more than 0.5 ppm for any month. A 1.5 ppm difference was observed when July temperatures caused a lowering of the dissolved oxygen concentration to 6.7 ppm (Fig. 2) at Station 1.

Tan and Van Engel's (1966) modification of the graphical analysis of Hubbs and Hubbs (1953) was used to test for significant differences in the means of substrate composition of Stations 1 and 2. By this method (Fig. 3), differences in the means are significant at a minimum of the 99% level if the solid and cross-hatched bars ($t_{0.05}x$ standard error either side of the mean) do not overlap and the hollow bars (one standard deviation either side of the mean) do. Significant differences at the 95% level are indicated if the solid and cross-hatched bars overlap, but do not overlap one of the means. If one of the means is overlapped by a solid or cross-hatched bar, no acceptable significant difference is shown.

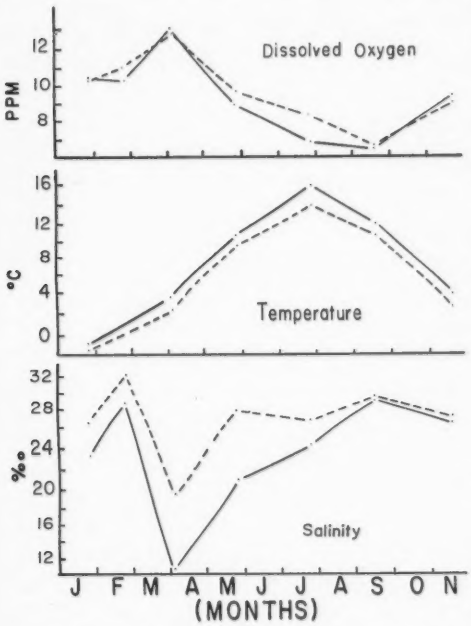

FIG. 2. Hydrographic data from bottom of water column at Station 1 (solid line) and Station 2 (dashed line).

Figure 3 shows significant differences between Stations 1 and 2 at the 99% level for all sediment fractions but coarse sand. Station 1 can be characterized by its predominance of fine sand. Granule gravel usually made up more than 50% of the sediment volume of Station 2.

Sawdust comprised 14 and 15% of the total sample volume of Stations 1 and 2, respectively (Fig. 3). These figures represent the sum of the mean percent sawdust concentrations of the sample fractions. Major differences in sawdust concentrations can be seen if the sawdust component is considered as a percentage of particular sample fractions rather than as a percent of the total sample. This can be achieved by dividing the mean sawdust component by the sum of the means of the sediment and the sawdust components of a particular fraction. For example, sawdust accounted for 31% [(6/13 + 6) 100] of the coarse sand fraction from Station 2 and 26% [(5/14 + 5) 100] of that fraction at Station 1. One-half of the fine sand fraction from Station 2 was sawdust, but only 17% from

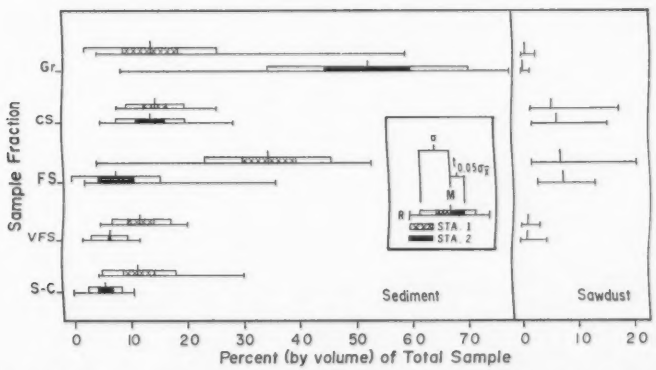

FIG. 3. Mean and range of both sediment and sawdust concentrations and the standard deviation and $t_{0.05}x$ standard error of the sediment concentrations. Differences in the means of sediment concentrations for Station 1 (Sta. 1) and Station 2 (Sta. 2) are significant at the 99% level if the solid and cross-hatched bars ($t_{0.05}\bar{\sigma}_{\bar{x}}$) do not overlap. Sample fractions are indicated as Gr, granule; CS, coarse sand; FS, fine sand; VFS, very fine sand; S-C, silt-clay.

Station 1 was sawdust. The very fine sand fraction was 14% sawdust at Station 2 and 8% at Station 1. The proportion of sawdust was higher at Station 1 only in the granule fraction. The silt-clay fractions from the stations did not have measurable amounts of sawdust.

Sixty-two species (or higher taxa) were identified from the year's collection. The species represented 19 families of Polychaeta, 10 families of Crustacea, and three families of Mollusca. One species each of Echinodermata and Pycnogonida were collected. Oligochaeta, Nematoda, and Nemertea accounted for most of the organisms not identified to species.

Eleven species (or higher taxa) were collected only from Station 1, and 15 only from Station 2. An average of 534 organisms/0.1 m² were collected

TABLE 1. Organisms collected from Stations 1 and 2 and calculated bio-indices.

		Collection date								
	Sta.	Jan.	Feb.	Apr.	May	June	July	Sept.	Nov.	Mean
No. of individuals/0.1 m²	1	383.5	2.6	9.3	230.9	326	252.7	809.3	875	361.2
	2	224	–	4	28.7	120	165.5	367.5	474	172.7
No. of species	1	21	2	3	18	13	27	22	32	17.3
(or higher taxa)	2	19	–	1	11	13	22	34	27	14.5
Bio-index	1	18.3	1.3	3.1	12.8	25.1	9.3	36.8	27.3	16.8
	2	11.8	–	4	2.5	9.2	7.5	10.8	17.6	8.0

TABLE 2. List of species from Stations 1 and 2 ranked by weighted mean percent ($\overline{X}_w$%) showing the accumulated percent by number ($\sum$ %by no.) and mean percent composition ($\overline{X}$% composition).

Rank	Organism	$\overline{X}_w$%	$\sum$% by no.	$\overline{X}$ % composition
	Station 1			
1	*Scolecolepides viridis*	285.0	12.4	19.0
2	*Macoma balthica*	180.0	20.3	12.0
3	*Mya arenaria*	169.6	22.6	11.3
4	*Polydora* sp.	80.6	30.7	6.2
5	*Mytilus edulis*	77.4	48.3	8.6
6	*Heteromastus filiformis*	65.9	53.8	5.1
7	*Pygospio elegans*	54.2	57.2	7.4
8	*Corophium volutator*	45.4	62.7	4.5
9	*Balanus balanoides*	33.3	70.9	6.7
10	Nematoda	21.7	74.4	2.0
11	*Aglaophamus* sp.	19.3	78.6	2.8
12	*Nephtys incisa*	18.2	80.9	2.6
	Station 2			
1	*Prionospio malmgreni*	180.8	27.4	15.1
2	*Corophium volutator*	158.9	35.8	11.4
3	Nemertea	115.9	46.4	10.5
4	*Polydora* sp.	49.0	51.1	4.9
5	Oligochaeta	48.0	58.7	3.7
6	Nematoda	46.0	63.0	4.0
7	*Gammarus lawrencianus*	39.6	63.5	13.2
8	*Scolecolepides viridis*	22.0	67.7	5.5
9	*Phoxocephalus holbölli*	21.3	72.1	2.4
10	*Aricidea jeffreysii*	20.3	78.8	2.9
11	Capitellidae (unid.)	16.5	82.5	2.4

per month from the two stations combined. Of these, an average of 361 (> 66%) came from Station 1 (Table 1). That more individuals per species were found at Station 1 can be seen from the mean bio-indices from Station 1 (16.8) and Station 2 (8.0).

The top-ranking species from both Station 1 and Station 2 (Table 2) had mean percent compositions of at least 10% at their respective stations. The dominant species from Station 1 (*Scolecolepides viridis*, *Macoma balthica*, and *Mya arenaria*) were found more frequently but not in as great numbers as the three dominant organisms from Station 2 (*Prionospio malmgreni*, *Corophium volutator*, and Nemertea).

The mean percent composition of *Gammarus lawrencianus* from Station 2 (Table 2) is unrealistically high. This species was the only organism found at Station 2 in April, which consequently raised the mean percent composition to 13.2%, and this is disproportionate to the number of specimens collected and the frequency with which they were found.

Discussion

Although many species were common to both stations in the Penobscot estuary, the differences between the communities were distinct. Monthly bio-indices (Table 1) summarize the general character of the stations. The mean bio-index of Station 1 was twice that of Station 2 due to the well-defined population peaks of *Heteromastus filiformis*, *S. viridis*, *M. balthica*, *Pygospio elegans*, *Aglaophamus* sp., and *Mytilus edulis*. The dominant species of Station 2, with the exception of *P. malmgreni*, did not have obvious population peaks at the times of sampling.

The association of Station 1 species (Table 2) has been previously found in the Penobscot estuary (Hartman 1960; Haefner 1967) and the Sheepscot estuary (Stickney 1959) under similar hydrographic and substrate conditions. However, the Station 2 community, with *P. malmgreni* as the dominant organism (Table 2), does represent a departure from earlier Maine surveys. In the Penobscot, *P. malmgreni* was not found by either Hartman (1960) or Haefner (1967). In the Sheepscot River estuary, Hanks (1964) found most of the species recorded from Station 2 (Table 2), including *P. malmgreni*, but his collections came from 95% silty substrates rather than from granular sediments which characterize Station 2.

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Effects of Sublethal Concentrations of Sodium Pentachlorophenate on Growth Rate, Food Conversion Efficiency, and Swimming Performance in Underyearling Sockeye Salmon (*Oncorhynchus nerka*)

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WEBB, P. W., and J. R. BRETT. 1973. Effects of sublethal concentrations of sodium pentachlorophenate on growth rate, food conversion efficiency, and swimming performance in underyearling sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 30: 499–507.

Tests were performed at 15 C, *p*H 6.8, and dissolved oxygen values of 90–100% air saturation. Growth rate and conversion efficiency were measured by feeding a ration level of 15% body dry weight/day to underyearling sockeye salmon (*Oncorhynchus nerka*) held at sodium pentachlorophenate (PCP) concentrations of 0, 1.14, 1.99, 3.49, 7.16, 13.60, 27.73, 31.57, and 47.18 ppb. Swimming performance was measured at PCP concentrations of 0, 7.21, 19.00, and 50.00 ppb. The 96-hr LC50 was 63 ppb PCP. Growth rate and conversion efficiency were almost equally affected by PCP, the EC50 values being 1.74 ppb for growth rate and 1.80 ppb for conversion efficiency. This is approximately 2.8% of the 96-hr LC50. Swimming performance was unaffected by PCP at the concentrations used.

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Nous avons poursuivi ces essais à 15 C, à un *p*H de 6.8 et à une teneur en oxygène dissous de 90–100% de saturation de l'air. Nous avons déterminé le taux de croissance et l'efficacité de conversion de la nourriture en donnant à des saumons nerka (*Oncorhynchus nerka*) de moins d'un an une ration équivalente à 15% du poids sec du corps/jour. Ces alevins ont été maintenus à des concentrations de pentachlorophénate (PCP) de 0, 1.14, 1.99, 3.49, 7.16, 13.60, 27.73, 31.57, et 47.18 ppb. Nous avons mesuré la performance natatoire à des teneurs en PCP de 0, 7.21, 19.00, et 50.00 ppb. La LC50 (96 h) est de 63 ppb de PCP. Le PCP affecte à peu près au même degré le taux de croissance et l'efficacité de conversion, les valeurs de LC50 étant de 1.74 ppb pour le taux de croissance et 1.80 pour l'efficacité de conversion. Ceci équivaut à environ 2.8% de la LC50 (96 h). Aux concentrations utilisées, le PCP n'affecte pas la performance natatoire.

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IN reviewing the measurement of effects of sublethal toxicant levels on fish, Sprague (1971) re-emphasized that growth and swimming performance should be routinely measured as good stress indicators. Experimentally, and undoubtedly biologically, the two response systems have fundamental differences. Growth can only be adequately measured by long term tests and is likely to indicate net stress effects on most metabolic systems. Although performance may be considered within the same broad energetic framework of converting and utilizing body substance, its demands are immediate; any failings can be measured by short term tests.

These two response systems, swimming speed and growth (along with food conversion efficiency) were used as indicators of stress from sublethal concentrations of sodium pentachlorophenate.

Pentachlorophenate (PCP) and its sodium salt (NaPCP) possess bactericidal, herbicidal, and insecticidal properties. They are often used as defoliants or for protecting cut timber from wood-boring insects and fungal rots, acting as powerfull metabolic poisons for most organisms including fish.

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Materials and Methods

Fish

Cultured underyearling sockeye salmon (*Oncorhynchus nerka*) from Pitt River, British Columbia, were used in all tests involving growth, swimming performance, and acute bioassay. Yearling fish from the same run were also used, but for acute bioassays only. All fish were acclimated for at least 2 weeks to the following experimental conditions: temperature 15 C, dissolved oxygen between 90 and 100% air saturation, photoperiod 16 hr, and fresh water *p*H of 6.8. Fish were fed on Abernathy "dry" pellets containing from 10 to 20% moisture. Underyearlings were fed a reduced ration of 15% body dry weight/day (dry food basis), given in two equal portions at 0800 and 1600 hr. Yearlings were given excess food once a day.

Pentachlorophenate

Sodium pentachlorophenate (PCP) at the desired dose was prepared from a stock solution. The stock was made by dissolving 6.659-g analar pentachlorophenol in 25 ml molar sodium hydroxide, and diluting the resulting solution to 1 liter with distilled water. The stock contained 7.209-g sodium pentachlorophenate per liter (Alderdice 1963); it was kept in the dark and freshly made up every 2 weeks.

Test concentrations were selected on the basis of an acute toxicity-response curve (Fig. 1), constructed by standard methods with 95% replacement of tank volumes every 12 hr (Sprague 1969). Bioassay conditions were similar to those applied in subsequent tests, except that fish were starved for 48 hr prior to testing and were not fed during a test. The fish density was always less than 2 g wet body weight/liter water. The median lethal concentration killing 50% of a sample of fish in 96 hr (96-hr LC50) was 63 ppb PCP; a 21-day LC50 was estimated as 57 ppb PCP. The maximum PCP concentration selected for growth and swimming performance experiments was 50 ppb, approximately 80% of the 96-hr LC50.

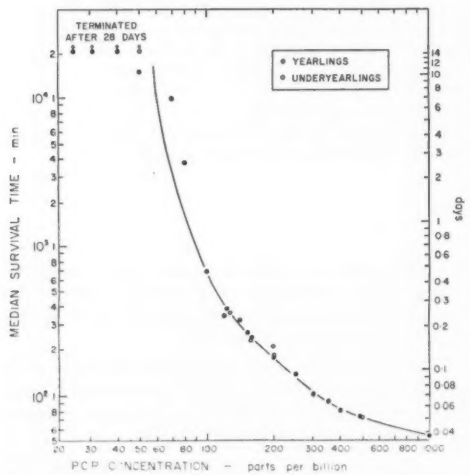

FIG. 1. Acute toxicity response curve for yearling and underyearling sockeye salmon (*Oncorhynchus nerka*) exposed to various concentrations of PCP. Points with arrows indicate tests terminated after 28 days with no mortalities. Each point represents a sample of 10 fish.

Growth Responses

Apparatus — Effects of PCP on growth rate and gross conversion efficiency were measured for two growth phases, a PCP-exposure phase of up to 8 weeks, and a 4-week postexposure phase. The same apparatus was used for each phase. Fish were held in 197-liter growth tanks (Brett et al. 1969) with a continuous water flow of 60 liter/hr. Water was circulated in each tank, and flow was approximately 20 cm/sec in the area of the tanks preferred by the fish. Input water was approximately 2 C below the required temperature, which was controlled at 15.0 ± 0.2 C by heaters. Dissolved oxygen levels were maintained close to air saturation by means of an air stone. During the exposure phase, automatic dosing apparatus (Velsen 1973) above each tank delivered the required PCP dose by appropriate dilution of the stock solution. The concentration was checked gravimetrically every other day.

Procedure — Following acclimation, 405 underyearlings of uniform size were selected and distributed randomly to six growth tanks. Five tanks contained 45 fish, one, 180 fish. A further 150 fish were set aside for swimming performance tests.

A previous study of the effects of whole bleached kraftmill effluent (BKME) on the growth of underyearling sockeye (Webb and Brett 1972) had indicated the desirability of continual review and updating of such experiments to use the available space and time most efficiently. This was made possible by subsampling from the larger group of fish, the remainder being the control sample.

Growth rates and conversion efficiencies were measured for 6 weeks after the initial distribution of fish to ensure there was no difference between the various growth stations.

PCP-exposure phase — One control and eight PCP concentrations were used — first 1.14 ± 0.15, 1.99 ± 0.04, 3.49 ± 0.20, 7.16 ± 0.11, and 31.57 ± 0.38, followed by 13.60 ± 0.06, 27.73 ± 0.31, and 47.18 ± 0.59 ($\bar{X}$ ± 2 SE) ppb PCP. Fish exposed to 1.14 ppb were terminated after 14 days and a subsample from the control group started at 13.60 ppb in the same tank. Similarly, fish at 1.99 ppb were terminated after 21 days and a new subsample started at 47.18 ppb. Fish exposed to 31.57 ppb died accidentally (mechanical malfunction) so another subsample was restarted at a similar dose level (mean 27.73 ppb).

Control fish, and those exposed to PCP concentrations of 3.49, 7.16, 13.60, 27.73, and 47.18 ppb were continued into the postexposure phase.

Sampling — At 14-day intervals (or when a group was terminated) fish were lightly anesthetized, weighed to the nearest 0.01 g, and length was measured to the nearest 0.1 cm. At 28-day intervals, or at the start or termination of any group, a random sample of 10 fish was air-dried at 60 C to minimum dry weight (approximately 72 hr). Food dry weight was determined in the same way. From these data, specific growth rate, ration, and gross conversion efficiency were calculated.

Analysis of data — Data were analyzed by graphic methods described by Webb and Brett (1972) for the estimation of median effective concentrations (EC50) above which PCP would be expected to reduce growth. The method takes into account the normal decrease in growth rate and conversion efficiency that occurs with increasing size. Thus, values measured for any group of fish exposed to PCP were compared with expected values for control fish of the same weight. The effect of the toxicant was calculated as a percentage of the measured response divided by the expected response.

As in the previous study of sublethal stress (Webb and Brett 1972), where effects close to threshold toxicant levels are of undoubted biological importance, although not necessarily statistically significant, and where complete numerical data are not readily available, the best estimate of the threshold or inflection point was deduced. The experiment was designed to be flexible so that appropriate concentrations could be tested as results accrued. Weights of fish in the various groups varied because of differences in starting times, and because of reduced growth following PCP exposure (see Table 1). Consequently, some of the basic data were not amenable to comparison by standard statistical treatment.

Swimming Performance

Swimming performance was measured in a tunnel respirometer by the system of increasing velocity steps, terminating at a fatigue velocity (Brett 1964, 1967). Test fish were held under the same conditions and fed the same ration as fish used in the growth experiments, and

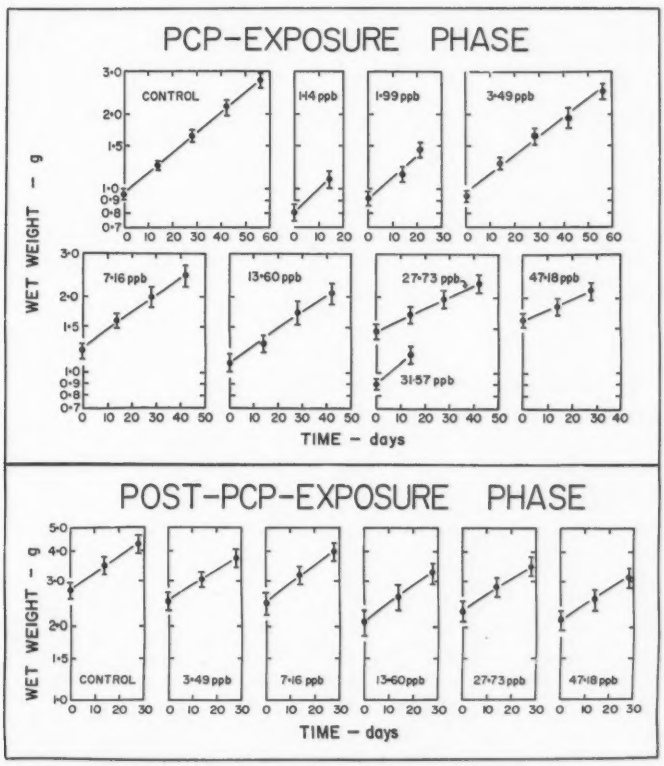

FIG. 2. Wet weight ($\bar{X} \pm 2$ SE) increases in underyearling sockeye salmon during and after exposure to various sublethal PCP concentrations.

TABLE 1. Summarized results of growth parameters for sockeye salmon (*Oncorhynchus nerka*) during and after exposure to various concentrations of sodium pentachlorophenate (PCP).

	PCP concentration ($\bar{X} \pm 2$ SE); parts/billion								
	Control	1.14±0.15	1.99±0.04	3.42±0.20	7.16±0.11	13.60±0.06	27.73±0.31	31.57±0.38	47.18±0.50
					PCP-exposure phase				
Duration (*days*)	56	14	21	56	42	42	42	14	21
Mean dry weight (*g*) for growth phase	0.379	0.192	0.257	0.363	0.417	0.345	0.227	0.436	0.446
Specific growth rate ($\bar{X} \pm 2$ SE) (% *dry weight/day*)	2.28±0.06	2.73±0.35	2.72±0.21	2.06±0.08	1.93±0.13	1.93±0.14	1.26±0.13	1.82±0.32	1.17±0.21
Ration (% *dry weight/day*)	14.6	15.2	15.0	14.7	14.3	16.1	14.6	14.1	14.9
Gross conversion efficiency (%)	15.6	18.0	18.1	14.0	13.5	12.0	8.6	12.9	7.9
					Post-PCP-exposure phase				
Duration (*days*)	28			28	28	28	28		28
Mean dry weight (*g*) for growth phase	0.917			0.798	0.822	0.661	0.721		0.645
Specific growth rate ($\bar{X} \pm 2$ SE) (% *dry weight/day*)	1.85±0.23			1.69±0.24	2.04±0.23	1.84±0.27	1.74±0.23		1.52±0.25
Ration (% *dry weight/day*)	14.5			15.0	14.6	15.0	14.6		16.6
Gross conversion efficiency (%)	12.8			11.3	14.0	12.3	11.9		9.2

were approximately the same weight as the fish in the PCP-exposure phase.

Water with the required PCP dose was flushed continually through the tunnel at 50 liter/hr from a header tank, fed by a single automatic dosing unit (as used in the growth experiment). The concentration was checked daily. Flushing at the required concentration was begun 12 hr prior to placing the fish in the tunnel. Fish were then held at the same dose for 2 days without being fed, prior to measurement of swimming performance.

The header tank and water tunnel were constructed mainly from plastics; it is possible that PCP is adsorbed on such surfaces. Bioassays performed at 100 ppb PCP showed that adsorption effects reduced the effective PCP concentration for the first 12 hr. The experimental procedure, therefore, took account of this; in addition, fish were pre-exposed to avoid possible excitement effects of sudden exposure. Random samples of 10 fish were tested for swimming performance at 15 C, with dissolved oxygen close to air saturation. Water velocity was increased from 10 cm/sec by 5-cm/sec increments every 60 min. The median fatigue time (FT50) was calculated with 95% confidence limits (after Lichfield and Wilcoxon 1949). Three replicate tests were made for control fish, and two at PCP concentrations of 7.21, 19.00, and 50.00 ppb.

Results

Growth Experiment

Weight changes — Wet weight increased in all groups of fish in both growth phases (Fig. 2). The logarithm of wet weight as a function of time could be approximated to a straight line.

During the experiment, the dry weight fraction of the fish increased significantly ($P < 0.05$); mean dry values were approximately 20% at the beginning of the PCP-exposure phase, and 28% at the end of the postexposure phase. Percent dry weight was weight related, such that fish from all groups had similar percent dry weights at the same wet weight (Fig. 3). Therefore, exposure to PCP had no direct effect on percent dry weight. All data were converted to dry weights for further analysis.

Growth parameters for the two growth phases are summarized in Table 1. Comparison between groups on a temporal basis is not valid, but must be done on the basis of equivalent weights. Therefore, from data given in Fig. 2 and 3, curves relating growth rate and gross conversion efficiency to dry

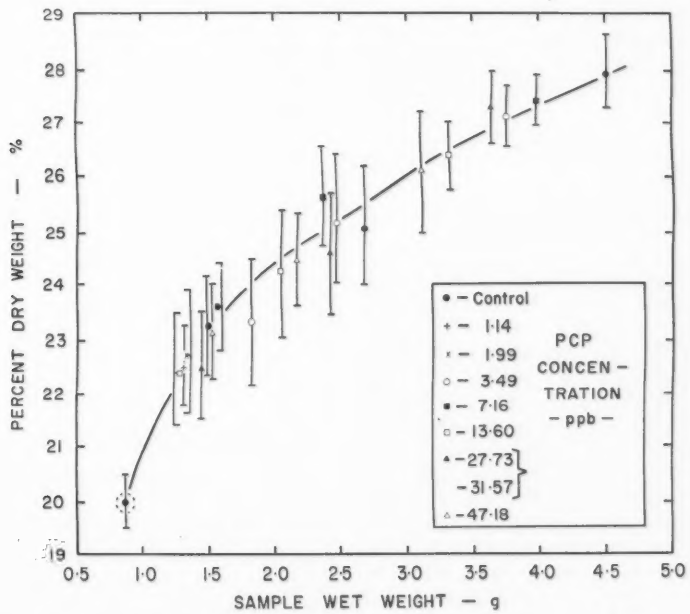

FIG. 3. Relation between changes in percent dry weight ($\bar{X} \pm 2$ SE; $n = 10$) and wet weight of fish sampled from all groups of fish during the course of PCP-exposure and post-PCP-exposure phases. The ringed point is the overall value for fish at the start of the PCP-exposure phase.

weight were constructed for each 14-day growth period for the control fish (Fig. 4A and C). Mean values for growth rate and conversion efficiency for the groups exposed to PCP can then be compared with the control curves (Fig. 4B and D). Both growth rate and conversion efficiency were reduced in the PCP-exposure phase at concentrations greater than 2 ppb and, to a lesser extent, in the postexposure phase. Some recovery was apparent in the latter growth phase.

Threshold levels of PCP — Expected growth rates and conversion efficiencies were taken from control curves in Fig. 4. Percent (measured/expected) va'ues were computed from results given in Table 1, and plotted against PCP concentration. For the PCP-exposure phase (Fig. 5) no decreases in growth rate and conversion efficiency were found at concentrations of 0, 1.14, and 1.99 ppb; in fact, both were elevated at 1.14 and 1.99 ppb PCP, a not uncommon feature that cannot at present be explained (see Sprague 1971; Webb and Brett 1972). Both growth rate and conversion efficiency were reduced at the higher PCP concentrations, as also observed by Kreuger et al. (1968) for *Cichlasoma bimaculatum*.

Significant dose/effect correlations were found between growth rate and conversion efficiency responses expressed as functions of the logarithm of PCP concentration ($r = 0.09$ and 0.91, respectively; $P < 0.05$), thus:

$$\text{percent (measured/expected growth rate)} = 0.112 - 0.323 \pm 0.787 \cdot \log \text{PCP concn}$$

$$\text{percent (measured/expected conversion efficiency)} = 0.111 - 0.322 \pm 0.755 \cdot \log \text{PCP concn}$$

Therefore, the percentage reduction in growth rate and conversion efficiency was similar at the same PCP concentrations.

The best estimate of threshold levels of PCP was taken as the intersection point between dose/effect regression lines and a zero response level calculated from pooled data for controls and the groups not deleteriously affected by PCP i.e. 0, 1.14, and 1.99 ppb. For growth rate, the threshold level was 1.74 ppb PCP, and for conversion efficiency, 1.80 ppb.

For the post PCP-exposure phase, percent (measured/expected) response values indicated recovery in all groups affected by PCP (Fig. 6). However, recovery was not complete in 28 days in any group of fish. Reduced growth rate and conversion efficiency was still found in groups previously exposed to 13.60, 27.73, and 47.18 ppb PCP, but the reductions were less than those found during the exposure phase.

Swimming Performance

Figure 7 shows that there was no significant difference ($P > 0.05$) in swimming performance between the groups tested at various PCP concentrations. Values for mean time-to-fatigue (FT50) were compared with expected values predicted from Brett and Glass (1973) where

$$\log \text{swimming speed } (cm/sec) = 1.1289 + 0.6345 \cdot \log \text{length } (cm).$$

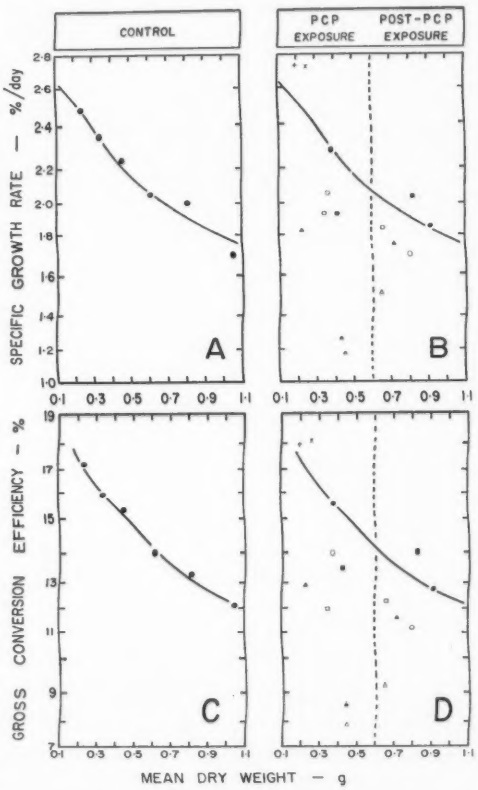

FIG. 4. (A) Relation between specific growth rate and dry weight for control fish, calculated for 14-day periods. Ration was 15% dry body weight/day. Curve fitted by eye (key as for Fig. 3); (B) Relation between the control curve in A, and mean values for growth rate of fish exposed to various concentrations of PCP; (C) Relation between gross conversion efficiency and dry weight for control fish; (D) Relation between the control curve in C and mean values for conversion efficiency calculated for various concentrations of PCP.

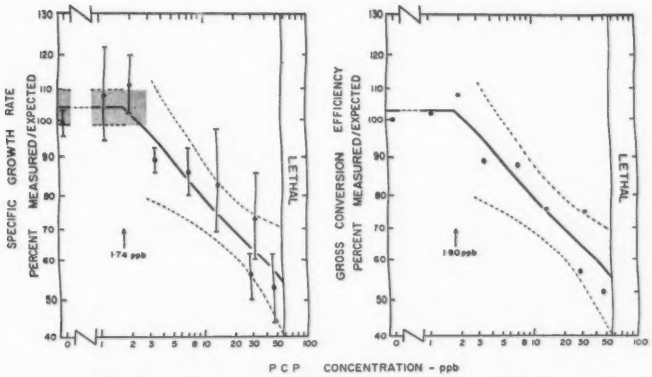

FIG. 5. Relation between growth responses (rate and efficiency), expressed as percent measured responses/expected responses, shown as a function of PCP concentration for the PCP-exposure phase. For growth rate, mean ± 2 SE are shown. The zero response level (just greater than 100%) was calculated from pooled data for fish exposed to 0, 1.14, and 1.99 ppb PCP, at which levels no effects of PCP could be detected. Shaded area shows ± 2 SE about this zero response level. Dotted lines indicate 95% confidence limits for mean response values, calculated for the linear regression relating response to PCP concentration. Vertical arrows indicate EC50 PCP concentrations. The vertical solid line indicates the estimated 21-day LC50, delimiting a lethal zone.

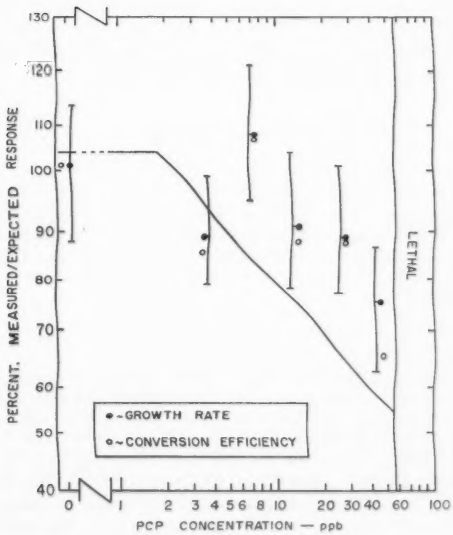

FIG. 6. Relation between growth parameters during the recovery phase and PCP concentration from the exposure phase. Responses are calculated as percent measured responses/expected responses for growth rate and conversion efficiency, and are shown in relation to the response line computed for the PCP-exposure phase shown in Fig. 5. Mean values, ± 2 SE, are shown for the growth rate relations only. The lethal zone is delimited by the 21-day LC50.

The indicated 95% confidence limits of ±8% of FT50 were assumed for the regression, this being the value given by Brett and Glass (1973) for fish in the weight range closest to that used here. The FT50 values all fell within these limits.

Discussion

Pentachlorophenate is classed as a general metabolic stressor, uncoupling oxidative phosphorylation (Garbus and Weinbach 1963; Nicholls et al. 1967; Boström and Johansson 1972). In fish and mammals, PCP increases mitochondrial metabolism while suppressing glycolytic activity (Kreuger et al. 1966; Kreuger and Liu 1970; Boström and Johansson 1972). Studies on *C. bimaculatum* indicated ATP levels were reduced (Kreuger et al. 1966). Elevated mitochondrial activity following PCP exposure resulted in high fat utilization in *Oncorhynchus kisutch* (Hanes et al. 1968) and *C. bimaculatum* (Pasley et al. 1968), and in elevated oxygen consumption in *Lebistes reticulatus* (Crandall and Goodnight 1962) and *Salmo gairdneri* (Chapman et al. 1968). Clearly, effects such as these could elevate main-

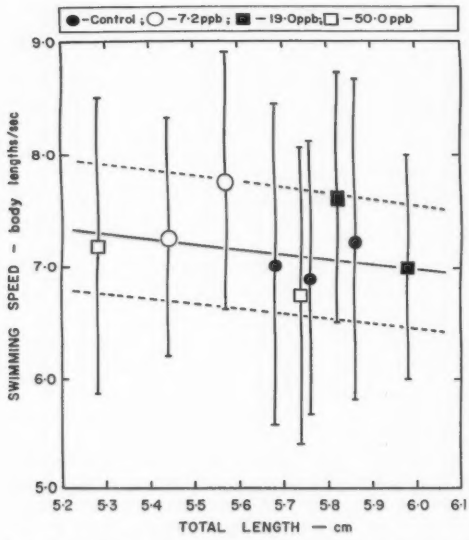

FIG. 7. Results of swimming performance tests for fish exposed to various concentrations of PCP, shown in relation to the mean length of fish tested. Performance is expressed as specific swimming speed (FT50 ± 95% confidence limits; $n = 10$). Solid line and dotted lines show the expected relation between performance and length, ± 95% confidence limits, calculated from Bretf and Glass (1973).

tenance energy demands of fish, reducing growth rate and conversion efficiency.

However, reduced growth rate could also result from a decrease in feeding or assimilation efficiency. This would be equivalent to a reduction in ration level. Brett et al. (1969) found that percent dry weight of the fish was related to ration level. Since percent dry weight was the same for fish in all groups (at comparable wet weights) in our experiments, the assimilated ration must have been the same and feeding and assimilation efficiency unaffected by PCP at the concentrations used.

Effects such as reduced ATP levels would also be expected to affect swimming performance. However, Sprague (1971) has noted that reduced swimming performance is often a symptom of direct interference with respiratory gas exchange. A general metabolic poison such as PCP is not expected to preferentially affect the gas exchange system, reducing swimming performance by this means. Nevertheless, the standard metabolic rate is elevated by PCP exposure (Crandall and Goodnight 1962; Chapman et al. 1968), while presumably the active rate is unaffected because swimming performance is not reduced; this is, of course, a common phenomenon in fish, where excitement often acts as a stressor (Brett 1964). Metabolic scope for activity would also be reduced. Sprague (1971) has suggested that reduction in scope could be a more sensitive indicator of stress than swimming performance.

For sockeye salmon, growth responses are obviously more sensitive indicators of stress than swimming performance; in practice, PCP levels above 50 ppb may well reduce swimming performance but, since 57 ppb would kill the fish within 21 days, tests at such concentrations would be of limited value. Kreuger et al. (1966) have listed several responses of *C. bimaculatum* in order of sensitivity to PCP. Growth was reduced before swimming performance, the latter only being affected at relatively high concentrations. Thus, in general, PCP concentrations likely to affect swimming performance are also likely to be high enough to eventually cause death.

Threshold (EC50) concentrations are commonly expressed in terms of application factor: EC50/96-hr LC50. The application factor for sockeye salmon based on growth responses was 0.028. Kreuger et al. (1966) state that growth rate in *C. bimaculatum* was reduced at about 27 ppb PCP, while the 96-hr LC50 for this species is of the order of 300 ppb (Kreuger and Chapman 1965). The application factor is thus of the order of 0.09. The sockeye salmon are clearly more sensitive to PCP poisoning in both relative (as application factor) and absolute terms.

Acknowledgments

This work was completed during the tenure of a National Research Council of Canada postdoctorate fellowship by P. W. Webb. Facilities were provided by the Fisheries Research Board of Canada, Pacific Biological Station, Nanaimo, B.C. Thanks are expressed by P. W. Webb to these organizations for their generous support.

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Optimum Economic Yield of a Fishery Given a Variable Price of Output

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ANDERSON, L. G. 1973. Optimum economic yield of a fishery given a variable price of output. J. Fish. Res. Board Can. 30: 509–518.

The majority of work done in the economics of fisheries uses the assumption of a fixed price of output. This paper describes the effects on the traditional fisheries model of relaxing this assumption, the most important of which, as far as regulation agencies are concerned, are the negation of marginal cost of effort equaling marginal revenue of effort as the criterion for a social optimum, and the introduction of the possibility of multiple equilibria and multiple industry profit maxima. Also, some new insights on fishery management with variable price and different assumptions about the number of fisheries and the number of countries involved are pointed out.

ANDERSON, L. G. 1973. Optimum economic yield of a fishery given a variable price of output. J. Fish. Res. Board Can. 30: 509–518.

Les travaux sur l'économique des pêches sont, pour la plupart, basés sur le postulat d'un prix fixe d'output. Nous décrivons dans le présent article les effets d'un élargissement de ce postulat sur le modèle traditionnel des pêches. Les modifications les plus importantes, en ce qui concerne les agences de règlementation, sont le rejet de concept d'un coût marginal d'effort égal à un revenu marginal d'effort comme critère d'optimum social, et l'introduction de la possibilité d'équilibres multiples et de maxima multiples de profit. Nous ouvrons également de nouvelles perspectives sur la gérance des pêches face à un prix variable, et attirons l'attention sur divers postulats concernant le nombre de pêcheries et le nombre de pays impliqués.

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FISHERY economics got its start in the middle fifties with the work of Gordon (1953, 1954) and Scott (1955). The most generally used model is an adaptation of the original papers and has been presented in works by Schaefer (1957) and Crutchfield and Zellner (1962). Recent works on the subject include those by Smith (1968, 1969) and Copes (1970). The former looks at the problem from the individual firm point of view as contrasted to the earlier work that was in terms of a whole industry. The latter shows the relation of the received doctrine to standard microeconomic analysis and, in doing so, allows for consideration of changing prices, something which has always been assumed away in earlier discussions. The present work is an attempt to extend the work of Copes and to show more completely its relation to earlier models using a geometrical model.

I believe work in this direction is useful even though it seems to ignore the work of Smith (1968, 1969). His very useful articles use a standard firm or a standard vessel as the basis of analysis. I think, however, that fishing effort is the proper unit of analysis in a general model. This allows the model to be applied in any instance by specifying what effort is. In some cases, it might be a standard firm or a standard boat; in others, it could be days out of port, days fishing, tonnage, etc. Moreover, for practical application in national or international fisheries management, a more aggregated look at the problem is almost a necessity. In addition, the fact that international fisheries management will be an important topic of discussion at the 1973 Law of the Sea Conference suggests that perhaps now is a good time to relook at aggregate models.

Production Function in a Fishery

The basis for understanding fishery economics is the population dynamics of an exploited fishery. What follows is a brief review of the subject. This section is included partly to stress the biological aspects of the

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problem. For a more comprehensive discussion see Beverton and Holt (1957) and Schaefer (1957).

The amount of fish that can be harvested per unit of time depends primarily on the level of fishing effort and the size of the fish population. Of primary interest is how much can be produced year after year given a certain level of effort, since effort is the only variable that can be controlled directly. However, since the population is dependent upon the size of the catch and, hence, the level of effort, a long run curve showing the relation between catch and effort can be constructed. Population will be in equilibrium when the amount caught is just equal to natural growth, which is a function of population size. The relation is graphically derived in quadrant 4 of Fig. 1 from quadrants 1, 2, and 3.

Quadrant 2 is the relation between population size and growth in weight (Q). There has been some discussion concerning the shape of this curve (Schaefer 1957). Is it symmetrical or does the rate of growth taper off more slowly than it grows? Quadrant 1 is the graphic representation of the set of combinations of population levels and fishing efforts that will yield a catch equal to the natural growth rate. It is drawn as a straight line using Schaefer's assumption of nondiminishing returns to effort at every level of population. As has been demonstrated by Carlson (1969), this relation would be graphically represented by a curve similar to the dotted one in quadrant 1 under the more economically realistic assumption of decreasing returns to effort. Southey (1972) has shown that there may be more than one level of population consistent with certain levels of effort. For simplicity, this possibility will be ignored.

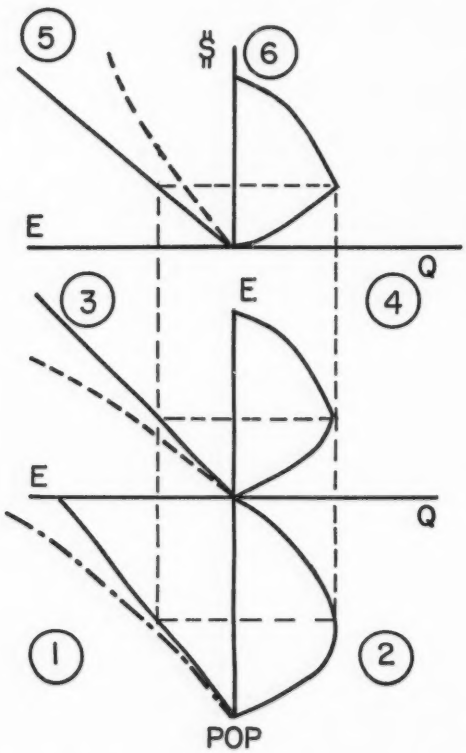

FIG. 1. The sustained yield curve in terms of effort (pictured in quadrant 4) can be derived from the relations between growth rate and population size and between fishing effort and population size (pictured in quadrants 1 and 2, respectively). Similarly, the relation between total cost and quantity caught (quadrant 6) can be derived from the sustained yield curve and the relation between effort and cost (quadrant 5).

Quadrant 3 is merely a transformation of axes. The curve in quadrant 4 can be constructed in the usual manner from the other three quadrants. Note that, because of the humped shaped of the growth curve, there are two levels of fishing effort that will catch each level of output except the maximum.

The curve in quadrant 4 is the derived sustained yield curve and it describes how much catch will be forthcoming from each level of effort each time period after the population level has adjusted to the fishing effort. This may take up to 7 years in some species. If either the growth curve is asymmetrical or there are decreasing returns to effort or both, then the sustained yield curve will be asymmetrical. Specifically, it falls more slowly than it rises. Although these points are important and they will change the shape of some of the curves to be discussed later, they will not change them enough to affect the results derived here. Therefore, a symmetrical sustained yield curve will be used.

Received Doctrine

A graphical model of the received doctrine is depicted in Fig. 2. The assumptions underlying it include: 1, A change in the output of the fishery will not change the price. This is assumed so because the fishery involved is

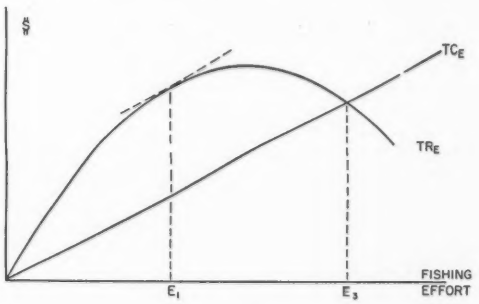

FIG. 2. The unregulated fishery will operate at E_3 where total cost equals total revenue. If price is constant, economic criteria would call for E_1 units of effort because at that point the marginal cost of a unit of effort is equal to the value of the fish caught by that effort.

considered to be one of many similar demersal fisheries. Although they are all of the same species, they do not migrate and so management of each can be carried on independently (Gordon 1954, p. 139, 146); 1a, sometimes the condition is stated such that industry price is constant or at least price elasticity is greater than 1 (Crutchfield and Zellner 1962, p. 14); 2, there is free entry and exit to the industry; 3, all natural conditions and biological relations are held constant; 4, gear selectivity is fixed; and 5, there is a linear relation between cost and fishing effort (this again is justified by the fact that we are dealing with one of many small fisheries).

This last assumption is not crucial to the analysis. An increasing total cost curve will yield the same general results but adds the complexity of dealing with intramarginal rents in an industry subject to regulation.

The total revenue curve as a function of effort (TR_E) as pictured in Fig. 2 is derived directly from quadrant 4 in Fig. 1. Its shape is guaranteed by either assumption 1 or 1a. The equilibrium level of fishing effort in an unrestricted fishery will be E_3 in Fig. 2. At levels of effort less than this, TR_E is greater than TC_E so existing units are encouraged to increase their effort and new people are attracted to the industry. The opposite analysis holds for points beyond E_3. E_3 is peculiar in that a reduction in effort and, hence, cost will result in an increase in output. If TC_E intersected TR_E to the left of maximum sustained yield, then this would not be the case.

According to the received doctrine, the socially optimal level of fishing effort is where the slope of the TR_E curve equals the slope of the TC_E curve (E_1). At this point, it is said, the last unit of product produced is equal in value to the last unit of input that produced it. As will be stressed later, the above is only true under the more restrictive assumption 1. The reason that the fishery does not operate at the socially optimal position is that no one owns it and the rent that is generated at this level will attract more effort until the rent is dissipated.

Relevance of Assumptions 1 and 1a

The relevance of assumption 1 may be challenged on the grounds that many commercially important species do indeed migrate and so the independent regulation of a series of small fisheries is not realistic in practice. Even if there are distinct small fisheries, the simultaneous management of all of them by a country or an international agency, which is more and more likely as time goes on, will mean that price cannot be considered a parameter.

To be sure that my use of the word relevance is not misunderstood, let me say that I do not question the consistency of the received doctrine on the basis of its assumption of fixed price. On the contrary, it is logically consistent and its conclusions are relevant to those cases where its assumptions hold. The discussion above, however, implies that it might be wise to investigate the implications of the possibility of a variable price of output.

The relevance of assumption 1a is brought into question by some recent empirical research by the Division of Economic Research of the National Marine Fisheries Service on the price elasticities of demand for various fish in the United States. Data provided on Canada were not as complete but did not significantly differ except for the case of sea scallops where the demand was elastic. Table 1 is a summary of the results.

As can be seen, all of the elasticities except those of Atlantic groundfish and halibut are in the inelastic portion of the demand curve. It is interesting to note that the actual derived elasticities of the above mentioned species were +0.1014 and −0.1571, respectively. An elasticity of −1.0 was used for purposes of the study because of the wrong sign of the derived number in the first case and its small size in the second case. (Two related points should be made about the data in Table 1. First, many of the species listed are nonmigratory in nature, but there is more than one fishery in each such case so the point about simultaneous regulation raised above applies. These species were included to show that an inelastic demand is not a special case to fish products, at least not in North America. Second, the elasticities given are for markets (groups of fisheries) and there is nothing inconsistent about an inelastic demand curve for a market and a fixed price for each fishery in it. However, if these fisheries are regulated as a unit, neither assumption 1 nor 1a is valid.)

The table shows that the assumption of elasticity of demand being greater than one is not a completely accurate portrayal of reality either, which means that models with less restrictive assumptions should be considered. (As will be shown in the next section, assumption 1a also causes some of the conclusions drawn from the traditional model to be incorrect.)

The fact that the assumptions concerning price do not always hold in practice, combined with the fact that regulation agencies draw what economic policies they do use from the traditional model, suggests that studying the implication of a variable price of output may be worthwhile.

TABLE 1. Price elasticities for selected species in the United States.[a]

Species	Estimated elasticity
Atlantic groundfish	−1.0
Halibut	−1.0
Northern lobsters	−0.5995
Sea scallops	−0.6337
Clams	−0.6047
Oysters	−0.6724
Shrimp	−0.3099
Crabs	−0.1487
Tuna	−0.8632
Salmon	−0.7066
Sardines	−0.9837

[a]Source: Bell et al. 1970.

Parzival Copes' Extension

Most economic analysis dealing with production is in terms of costs per unit of output rather than per unit of input as is the case of the standard economic analysis of a fishery. Copes (1970) makes this transformation and his analysis explicitly allows for the study of a variable price of output. He readily admits that he is not the first to draw a cost curve for a fishery in terms of output, but he was the first to show the direct relation between the received analysis and the standard microanalysis. The basis for his analysis is derived in quadrant 6 of Fig. 1 from quandrants 3, 4, and 5.

Quadrant 4 is the effort–output relation described earlier. Quadrant 3 is used for the transformation of axes and quadrant 5 is the cost–effort relation that is plotted in Fig. 2. (Ignore for the moment the dotted curves). Using these quadrants, a backward bending total cost curve for the fishery in terms of units of output (TC_Q) is derived in quadrant 6. It is not a cost function in the normal sense where each unit of output has a unique cost but, rather, a relation between cost and quantity. There are two levels of effort that will catch each quantity (except the maximum) and, hence, there are two levels of cost for each. Operating at a level of effort beyond the maximum sustainable yield is equivalent to operating at the higher level of costs for a specified output.

The average cost curve that is related to this cost curve and the marginal cost curve that is associated with its upward sloping segment are pictured in Fig. 4B. For an economic discussion on the backward bending total cost curve, the reader is referred to Tangri (1966), and for empirical studies of this type of curve in a fishery, to Bell (1972) and O'Rourke (1972).

Q_3 is the output that will be produced in an unregulated fishery that is expanding for the first time. Q_3' and Q_3'' will be explained later. In this regard Q_3 is equivalent to E_3 in Fig. 2 although, since Fig. 3 was drawn to demonstrate the special problem of multiple equilibria, Q_3 represents a level of effort to the left of maximum sustainable yield while E_3 is to the right of it. Points to the left of it have revenues higher than cost and so more fishing effort will be encouraged, which will bring about an increase in output. The opposite is true for points to the right of Q_3. It is important to note that, if the demand curve were higher, Q_3 would be produced in the backward bending part of the cost curve.

The socially optimal output is Q_2 produced at a cost of C_2 (i.e. at the lower of the two levels of effort that will yield Q_2). This output is socially optimal since at this point price is equal to marginal cost.

A firm holding monopolistic control over the fishery would operate where $MR_Q = MC_Q$ or at output level Q_1. This is the point of maximum rent.

Using Fig. 4B, it is possible to differentiate two types of rent. The rent that is earned by operating at $P = MC_Q$ (which can only be an equilibrium point under restricted entry) can be called the rent due to the uniqueness of the fishery. The increase in rent that accrues by moving to the point where $MR_Q = MC_Q$ may be called a monopoly rent.

It will be recalled that the traditional model concludes that the fishery should operate where the marginal cost of effort (MC_E) is equal to the marginal revenue of effort (MR_E) (i.e. at effort level E_1 in Fig. 2). This is equivalent to saying that marginal revenue of output (MR_Q) is equal to marginal cost of output (MC_Q).

Under assumption 1 of a constant price of output, $MR_Q = P_Q$. Therefore, in this case, the conclusion that the fishery should operate where $MC_E = MR_E$ is equivalent to $MC_Q = P_Q$ which is a social optimum. On the other hand, under assumption 1a of elasticity greater than 1, the conclusion that the fishery should operate where $MC_E = MR_E$ is the same as $MR_Q = MC_Q$ which is the monopolist position. Further, although assumption 1a listed above will guarantee that the revenue curve will be the shape specified, it will mean that the conclusion that operating where $MR_E = MC_E$ (i.e. point E_1 in Fig. 2) is a social optimum will be incorrect.

Put another way, this says that policy formulations based on the traditional, and only existing, model can be incorrect if assumption 1 does not hold. A variable price of output, whether demand is elastic or inelastic, will invalidate the model's conclusions.

For example, this means that the assertion that sole ownership of a fishery will result in an optimum allocation of resources, as is sometimes stated in the traditional models (Gordon 1954, p. 141, and Scott 1955, p. 124), is incorrect. Obviously, a sole owner would operate such that he could "collect" both types of rent described above. This means that regulation plans that call for issuing property rights to the fishery may not be optimal if the property rights are vested in one entity or in a "small" group of entities. This is not to say that Gordon and Scott were not aware of the possibility of the monopoly problem. They both explicitly state that they are, but their assumption of fixed price rules it out. This can be a weakness in extrapolating from their models to the practical situation.

A Revenue Curve with Two Maxima

By dropping assumption 1 (or 1a) in the received analysis and instead allowing the price of fish to vary without qualification as output varies, new insights may be gained. And when this analysis is used with that of Copes, a very complete picture of the economic aspects of a fishery may be obtained.

A graphical description of the effects on the total revenue curve of the relaxed assumption with respect to price is depicted in quadrant 9 of Fig. 3. It is derived from quadrants 7, 8, and 10. Quadrant 7 is the standard catch and effort curve. Quadrant 8 is used to transform the axes and quadrant 10 plots total revenue as a function of output, which can be derived directly from the demand curve. If the maximum output is higher than the output that generates maximum revenue, the total revenue curve as a function of effort (TR_E) will be double humped as is illustrated. I have chosen to call this particular type of revenue curve the Double Maxima Revenue Curve, hereafter called the DMRC. Although I have taken the liberty of naming this curve I do not claim to have discovered it. Schaefer (1957, p. 675) depicts such

a curve without a complete description of its underpinning or a discussion of its implications. In fact, throughout his discussion, he assumes price to be constant (assumption 1 above).

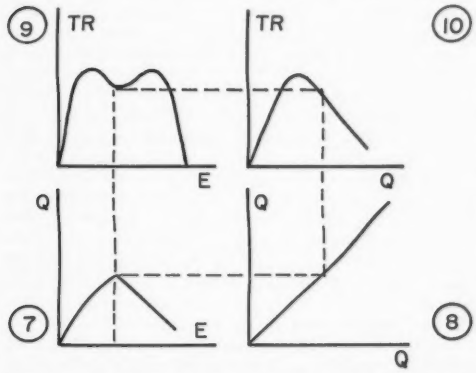

FIG. 3. The double maxima revenue curve (quadrant 9) can be derived from the sustained yield curve (quadrant 7) and the relation between total revenue and quantity sold (quadrant 10). Note that the maximum total revenue is reached at a catch level below maximum sustainable yield.

This curve will be symmetrical if the curve plotting the relation between growth and population size is symmetrical. The two equal maximum points will represent levels of effort that bring a quantity of output such that TR is a maximum. The minimum between the two humps is the level of effort that brings forth the maximum sustainable yield.

Before leaving this description of the DMRC, it should be stressed that a variable price (i.e. a standard downward sloping demand curve) is only a necessary condition for the DMRC. A sufficient condition is maximum output in the inelastic portion of the demand curve.

The introduction of the DMRC significantly changes the standard analysis (see Fig. 2) by adding the possibility of multiple equilibria in an unregulated fishery and of multiple profit maxima, one of which will be a global maximum. The works of Smith (1968, 1969), Copes (1970), and Southey (1972) describe the existence of multiple equilibria but not multiple profit maxima. Southey's analysis is based on multiple population levels consistent with certain levels of effort rather than with a variable price. Figure 4A graphically depicts some examples.

Cost curves 1, 2, and 6 allow for one equilibrium in an unregulated fishery and for the possibility of one

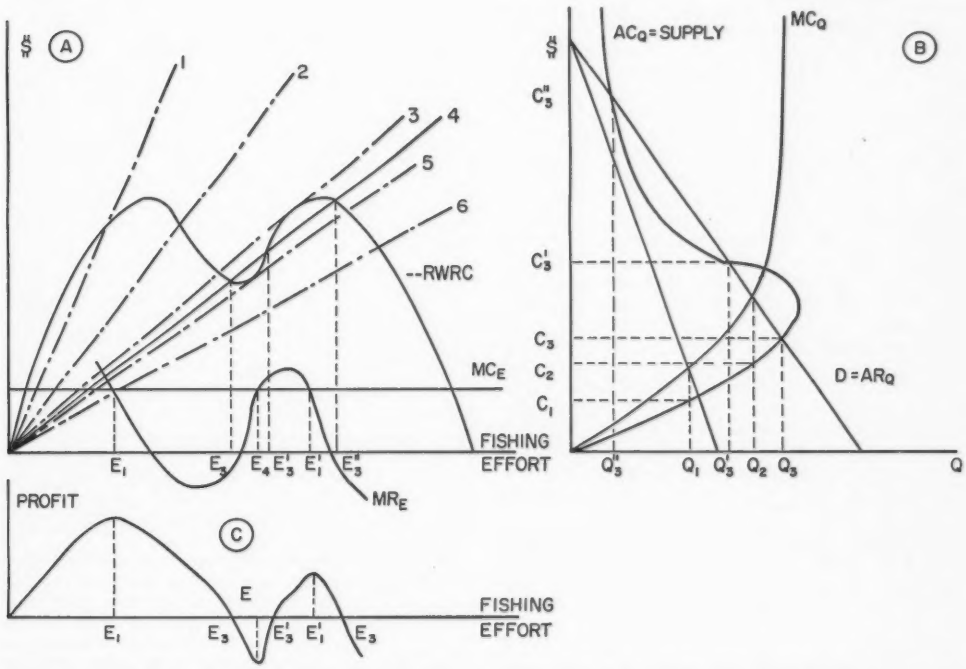

FIG. 4. A and B show possible equilibria of a fishery, A in terms of effort and B in terms of quantity caught. E_1 corresponds to Q_1 and C_1, etc. C shows the relation between profit and industry profit.

or two profit maxima depending upon the relative slopes of the DMRC and the cost curve. Curves 3 and 5 allow for two equilibria and for two profit maxima. Finally, cost curve 4 allows for three equilibria and for two profit maxima. Since the cost curve is drawn assuming the fishery is on the sustained yield curve (see Fig. 1), these are both economic and biological equilibria.

The interesting points of the analysis will be discussed in terms of cost curve 4, but the interested reader can do the same for any of the others.

By construction, the MR_E and the MC_E of curve #4 must intersect in three places. The same is true for cost curves 3 and 5 but not 1, 2, and 6. In the latter cases, there may be one or three intersections, or even one intersection and one tangency. This is why these cases only allow for the possibility of multiple profit maxima.

Figure 4B is the case of curve #4 in terms of the demand curve. Figure 4C is profit plotted as a function of fishing effort. E_3 (Q_3 with cost C_3), E_3' (Q_3' with cost C_3'), and E_3'' (Q_3'' with cost C_3'') are possible equilibria in an unregulated fishery. It is impossible to predict offhand which of the equilibria will be in effect at any given point in time, although it would be very useful information to a regulatory agency working with this fishery. As pointed out above, in a fishery expanding for the first time, Q_3 will probably be the existing one. The others may be possible depending upon historical changes in demand (see Copes 1970, p. 72) or upon the speed of entry or exit of boats from the fishery.

Strictly interpreted, the received doctrine calls for regulation where $MR_E = MC_E$. In a case such as this, however, not only is this bad advice since it is not equivalent to $P = MC_Q$, it is also confusing bad advice since the condition holds at three points (i.e. E_1, E_4, and E_1'). It is obvious, however, that, of these, only E_1 and E_1' meet the second order conditions for a profit maximum. The possibility of two such profit maxima must give regulatory agencies pause to think. In the real world of "muddling through" one may be at a point that satisfies a certain specification and yet may not be meeting the goal for which it was designed. That is, the fishery may be operating at say E_1' where there is a local positive profit maximum. Both slight increases or decreases in effort will reduce the level of profit. This would lead the managers to believe that they were operating correctly. In actuality there are two positions, not counting the one where $P = MC_Q$, that would be superior. One would be at E_1, where the profit is larger, and the other would be that level of effort to the left of maximum sustainable yield that produces the same level of output as does E_1'. At that point catch and revenue would be the same as at E_1', but cost would be less.

However, the main point of this paper is that operating where $MR_E = MC_E$ is optimal only under the restrictive assumption of a constant price of output. In the case presented here the socially optimum level of output is Q_2 with cost C_2 where MC_Q is equal to price.

This means that, although the level of fishing effort is the policy variable under the control of the regulatory agencies, the optimum output of a fishery can not easily be defined in terms of it if price is not a constant. Instead, analysis must be carried on in terms of average and marginal costs and the prices of output.

It is interesting to note that the level of fishing effort corresponding to Q_2 can not be found directly in Fig. 4A although, if a complete analysis such as Fig. 1 and 3 were used, it could be. Also, the fact that, when MC_Q is equal to P in the inelastic portion of the demand curve, E_2, the optimum level of effort, will be in the decreasing portion of the first hump of the DMRC should not confuse anyone. It is only revenue and not output that is falling as effort increases up to the optimum point. And, although revenue is falling, each extra unit still costs less than people are willing to pay for it. Along the same line, the levels of output corresponding to E_4 and E_1' are not obvious from Fig. 4B.

In summary, then, dropping the assumption of fixed prices or elastic demand curves yields the DMRC, which is a much more general analysis. It points out the possibility of more than one local profit maximization point and of multiple equilibria. It also shows that strict adherence to the conclusions of the traditional model when not all of its assumptions hold can lead to folly. (This is, of course, true for any model, but I think there is a very real possibility of it happening in the regulation of large fisheries, whether by national or international agencies.) When used with a Copes type analysis, the DMRC is useful for analyzing the level of effort and the level of output for the optimumly controlled fishery.

A Combined Analysis

It may prove useful at this point to study Fig. 1 and 3 as a unit. By doing so one can see the relation of the DMRC model and the Copes type model and the dependency of both on the population dynamics of the fishery. The level of effort determines the level of population and the level of cost, while the combination of effort and population size determines the level of output, which, given the demand conditions, determines the level of revenue.

The model can be made more general in two ways without affecting the analysis. First, if the assumption of a constant price of effort is dropped, the cost curve in quadrant 5 of Fig. 1 will be upward bending rather than a straight line.

Also, if it is assumed that there are some crowding externalities at high levels of effort, the change of axes line in quadrant 3 can be represented by a curved line that is increasing at a decreasing rate like the dotted one in the figure. This means that more and more units of effort will have to be used to get the same amount of increase in actual effort to the fishery as the level of effort increases. The changes will not significantly affect the shape of the other curves in Fig. 1 or 3.

The relation between Smith's model and the above can also be demonstrated. The curve in quadrant 1 is his population equilibrium curve. (Smith 1969, p. 87. See also Fullenbaum et al. 1971.) If one were to draw in his industry equilibrium curve in the same quadrant, it would intersect the population equilibrium curve as many times (representing the same levels of effort) as the demand curve would intersect the average cost curve

derived from the total cost curve in quadrant 6 of Fig. 1 and as many times as the total cost curve would intersect the revenue curve in quadrant 9 of Fig. 2. It is not possible, however, to use Fig. 1 to relate other points on the industrial equilibrium curve to the present discussion since it is based on long run population equilibrium.

Regulation Analysis with a Variable Output Price

The received doctrine deals with only one small fishery in a world of many similar ones so that price can be considered a parameter. It asserts (and rightly so under these assumptions about prices) that the social optimum is where $MR_E = MC_E$.

Little analysis has been given to the regulation of many small fisheries by one country or to the regulation of one big fishery or many small ones by many countries. In the latter case it is said that no generalization can be made since each country will more than likely have different demand and cost conditions as well as different national goals or social institutions or both (Christy and Scott 1965). The statement is generally true but, using the analysis presented by Copes, some specific cases can be examined in detail.

Case I: Many Small Fisheries Contained Under National Control

There are actually two possible subcases here. One is when each small fishery has its own unique effort market and it is impractical to shift effort among fisheries. The second is when effort can be shifted from area to area with ease. Gordon (1953, p. 131; 1954, p. 450) analyzes this case in greater detail. The first subcase is actually the second in the short run. The analyst may want to use the first subcase in his analysis if he feels that the social cost of shifting effort is too high. In either case each fishery will have a set of cost curves similar to those developed by Copes.

In the first subcase these curves follow our analysis directly. The second case requires further analysis, however. This is so because, if all fisheries are not equidistant from the port, there will be different transportation costs for each fishery and, if the supply curve of fishing effort is upward sloping, the cost in any one fishery will depend upon the level of fishing effort in the other fisheries.

Figure 5 is a graphical means of solving the above problems. The key to the solution lies in the fact that marginal productivity of effort must be the same in all areas to achieve maximum efficiency.

Assume there are two fisheries with the fishery production functions $Q_1 = a_1E_1 - b_1E_1^2$ and $Q_2 = a_2E_2 - b_2E_2^2$. (These production functions are of the type derived by Schaefer (1957, p. 673). Although this seems to ignore the size of the population, it in fact does not. Population is determined by the level of effort and so, for each level of effort, there is a level of population consistent with it. (Other production functions that deal more directly with population, such as the ones implicit in the discussions of Gould (1972) and Southey (1972), would make the analysis to follow unnecessarily complex). The following must hold at all times in order to achieve efficiency: $a_1 - 2b_1E_1 = a_2 - 2b_2E_2$.

Therefore, under these same circumstances, E_2 will always equal $\frac{a_2 - a_1}{2b_2} + \frac{b_1}{b_2} E_1$ and so total fishing effort can be expressed in terms of E_1 as Total Effort $= E_1 + \frac{a_2 - a_1}{2b_2} + \frac{b_1}{b_2} E_1$.

It is this curve that is plotted in the southeast quadrant of Fig. 5. I have drawn it using the assumption that a_2 is greater than a_1; that is, that the marginal productivity of effort is higher in area 2 than in area 1 at lower levels of effort in each. This means it is not profitable to add effort to area 1 until enough units ($\frac{a_2 - a_1}{b_2}$ in this case) have been used in area 2 to reduce the productivity there to that of the first effort used in area 1. The southwest quadrant is a transformation of axes curve and the northwest quadrant is the supply curve of labor at a fishing area shifted up horizontally by T_1, the average transportation cost to fishing area 1. Using these three quadrants it is possible to derive a supply curve of effort to fishery #1 assuming that effort is expanded such that the efficiency conditions hold. For example, by selecting fishing effort equal to E_1' in area #1, the total amount of effort can be found by tracing to the southeast quadrant. By tracing up into the northwest quadrant the supply price for this level of total effort can be found. This added to T (which is done automatically in the diagram) gives the supply price of E_1' under the conditions of efficiency. Other points on this supply curve can be constructed in a similar manner.

Using this supply curve, a total cost curve for effort can be constructed for area #1, which can then be used in the normal manner to construct its cost curves similar to those in Fig. 4B. This same procedure can be used for each individual fishery. (The graphical analysis is in terms of two fisheries, but the extension to many involves only more mathematics to construct the curve in the southwest quadrant of Fig. 5).

The horizontal sum of the marginal cost curves in each of these fisheries is the socially optimal supply curve. Where it intersects the market demand curve is the socially optimum output for all the fisheries. Each fishery, however, must operate where its marginal cost is equal to price. In Fig. 6, $\overline{X}_1$ is the socially optimum total output and X_1 is the socially optimum output for one representative fishery. (Ignore for the moment the demand and marginal revenue curve in the left hand graph.)

The problem for the regulation agency in this case is twofold. First, it must choose the combination of price and quantity that will be socially optimal. Second, it must decide the most efficient way to produce the optimal output; that is, it must determine the level of output from each of the small fisheries.

The optimum output and price can be determined by constructing the socially optimal total supply curve from the marginal cost curves of each of the small fisheries. The intersection of the market demand curve with this

supply curve yields the optimal total output and the price. Once this price has been determined, the agency can use it as a parameter to determine the optimum amount of output from each fishery.

This procedure will guarantee the same results as would the case where many small fisheries (enough so that none has an influence on price) are regulated individually according to the conclusions of the traditional model. In that case, each fishery would consider its MC_Q as its socially optimal supply curve. The industry supply curve will be the sum of these. Acting independently, they would determine the price that would determine the level of output from each of them.

I emphasize this to reenforce my point that the traditional model, using assumption 1, is logically consistent. In cases where price can not be considered a constant, however, regulation agencies must take this fact into consideration in the manner described above.

Case II: A Significant Part of a Fishery (or a Significant Number of the Total Small Fisheries) is under National Control

In this case the nation has an effect on price but does not have absolute control. (The nation's market power is somewhere in between that of Case I and the standard assumption of no power over price.)

A demand curve for a nation in this situation can be constructed by subtracting the amount the rest of the world will supply at each price from the world demand curve. If the marginal cost curve of the nation's fishery (or the sum of the marginal cost in the case of many fisheries under national control) is placed on the same diagram as this demand curve, the country has a basis for allocating its fishing effort.

One must be very careful when talking about a social optimum in this case since, by assumption, the rest of the world may not be operating efficiently. The country

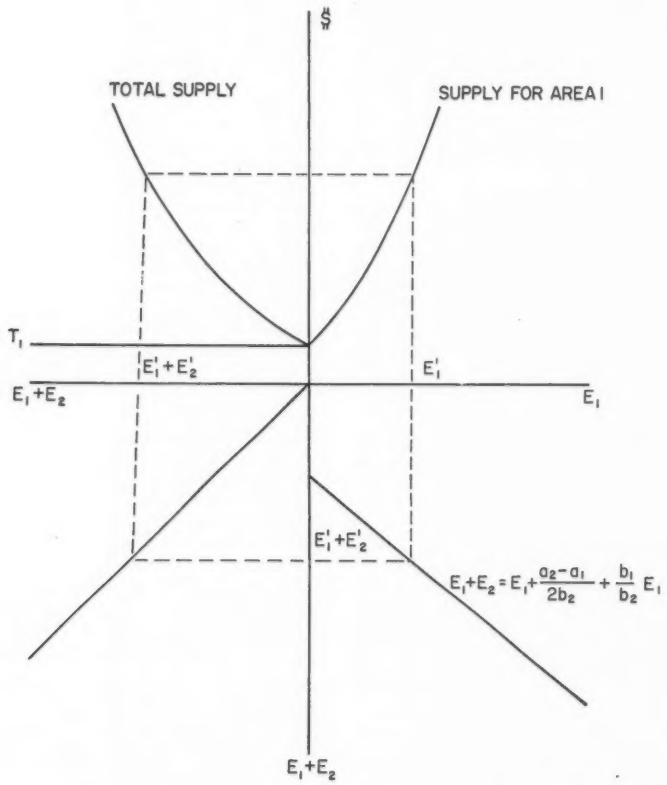

Fig. 5. The supply curve of effort for one of two related fishing areas can be derived using the efficiency relation between E_1 and $E_1 + E_2$ and the total supply for both areas.

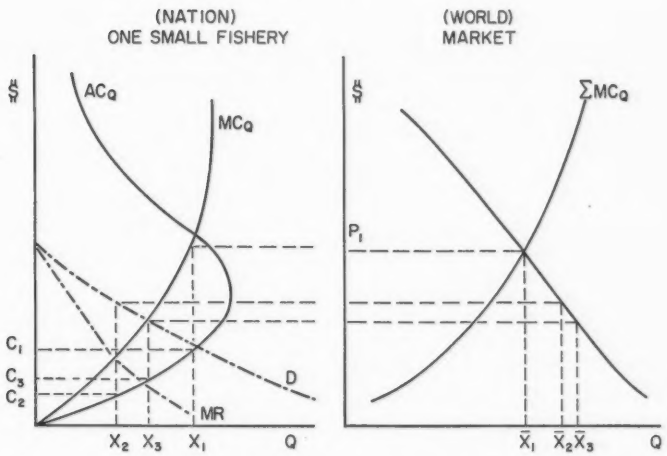

FIG. 6. The supply curve for the market ($\sum MC_Q$) is the horizontal sum of its individual fisheries. The optimal amount for the market is $\overline{X}_1$ and the optimal for a representative small fishery is X_1.

has two main alternatives open to it. First, it can take advantage of its semimonopoly power and restrict output such that it earns monopoly rents. In this case, it would operate such that $MR_Q = MC_Q$.

As an alternative, it can extend output until $MC_Q = P$; that is, until the value of the marginal product equals MC_Q. In this case there would be more fish available, yet the country would not be using its resources to produce fish if they were more productive elsewhere (i.e., if the fish could be captured more efficiently elsewhere). Which of these alternatives it chooses would depend in part upon whether it is a large exporter or a consumer of fish.

The point can be illustrated by using Fig. 6 again. In the right hand graph think of $\sum MC_Q$ as the supply of the rest of the world and the demand as world demand. The demand curve in the left hand graph is the nation's derived demand. $\overline{X}_2$ and X_2 are the world's output and the country's output, respectively, if the country uses its monopoly power. On the other hand, if the country uses its locally efficient level of output, the world's output will be $\overline{X}_3$ and the country's output will be X_3.

How much is purchased by the country under consideration depends upon its demand curve, which is a part of the world demand curve.

The above procedure would not be proper if the country had another goal, such as maximizing the level of employment, rather than efficiency.

Conclusions

The received doctrine is a specific case of the general model presented here. Some of the conclusions derived from the specific model can not be generalized, especially the conclusion that the optimum social rate of output is where marginal revenue of effort is equal to the marginal cost of effort. Regulation agencies, both national and international, should bear this in mind when formulating their policies.

It should also be kept in mind that empirical investigation based on the general model will be very difficult. Estimates of the yield and cost per unit of effort are at best averages and the dispersion around these averages may be quite large (Hutchings 1967). The problems involved in constructing demand curves are well known. It appears then that the other curves that are constructed using the production, cost, and demand curves as a basis may be less than completely accurate. This, of course, is not a weakness of the model itself, however, but it points out that it should be used with care.

Acknowledgments

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Crustacean Plankton and the Eutrophication of Lakes in the Okanagan Valley, British Columbia

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In early September 1969 and late August 1971, the vertical and horizontal distribution of temperature, Secchi disc visibility, some chemical components, and zooplankton abundance in lakes Okanagan, Skaha, and Osoyoos were investigated. In addition, lakes Kalamalka and Wood were sampled only in late August 1971. Four different basins could be distinguished in Lake Okanagan: the Penticton-Summerland basin, the Peachland-Kelowna basin, a basin north of Kelowna, and one formed by the northern end of the lake. Total dissolved solids, calcium, and electrical conductivity within the lake decreased gradually from north to south. Macroelement values within lakes Okanagan, Skaha, and Osoyoos were apparently not substantially different but Kalamalka and Wood lakes were about twice higher in sodium, potassium, magnesium, and about 1.5 higher in total dissolved solids. Four species of copepods and nine species of cladocerans were found with *Cyclops bicuspidatus thomasi* and *Diaptomus ashlandi* dominant in all five lakes. *Diaphanosoma leuchtenbergianum* and *Daphnia longiremis* were the most common cladocerans in all five lakes. Also, *Daphnia thorata* was common in all except Wood Lake. Eighty-nine percent of the total plankters in Lake Okanagan were located in the upper 50-m layer. Relatively little horizontal variation was found within the lake but two areas, near Kelowna and in the northern end showed in both years of investigation greater abundance of plankton than the remaining areas. Crustaceans were usually less abundant inshore than offshore. Volume of settled net plankton varied from 8 mm^3/cm^2 in Okanagan Lake to 31 mm^3/cm^2 in Wood Lake. No substantial changes in species composition of zooplankton, Secchi disc visibility, and dissolved oxygen in the hypolimnion were found relative to the data of 1935 reported by Rawson. However, in 1969 and 1971 net plankton volumes were about five and three times larger, respectively, than in 1935. Calculations of total phosphorus load from two independent sources of data provided similar results and indicated that lakes Okanagan and Kalamalka are still in the oligotrophic range but close to mesotrophy. Lake Wood is moderately eutrophic and lakes Skaha and Osoyoos showed a marked degree of eutrophy, higher than in Lake Washington, U.S.A. before sewage diversion, or in Lake Erie. The estimates for lakes Wood, Skaha, and Osoyoos were supported by the values of the hypolimnetic areal deficits characteristic for highly eutrophic lakes. The trend of changes in phosphorus load during the past century is presented and predictions are made about the load in 1990 in situations with and without phosphorus removal from sewage.

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Au début de septembre 1969 et à la fin d'août 1971, nous avons étudié la distribution verticale et horizontale des températures, la visibilité du disque de Secchi, quelques constituants chimiques et l'abondance du zooplancton dans les lacs Okanagan, Skaha et Osoyoos. En plus de ceux-ci, les lacs Kalamalka et Wood ont été étudiés en fin d'août 1971 seulement. Nous avons pu identifier quatre bassins distincts dans le lac Okanagan: le bassin Penticton-Summerland, le bassin Peachland-Kelowna, un troisième au nord de Kelowna et enfin un quatrième formé par l'extrémité nord du lac. Il y a diminution graduelle du nord au sud des solides totaux dissous, du calcium et de la conductivité électrique. Les concentrations de macro-éléments ne semblent pas différer appréciablement dans les lacs Okanagan, Skaha et Osoyoos. Par contre, les lacs Kalamalka et Wood ont des teneurs environ deux fois plus élevées en sodium, potassium et magnesium, et 1.5 fois plus élevées en solides totaux dissous. Nous avons trouvé quatre espèces de copépodes et neuf de cladocères, avec prédominance, dans les cinq lacs, de *Cyclops bicuspidatus thomasi* et *Diaptomus ashlandi*. *Diaphanosoma leuchtenbergianum* et *Daphnia longiremis* sont les cladocères les plus communs dans les cinq lacs

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étudiés. De plus, *Daphnia thorata* est commun dans tous les lacs, sauf le lac Wood. Dans le lac Okanagan, 89% de tous les organismes planctoniques se trouvent dans les 50 m supérieurs. La distribution horizontale ne varie que très peu dans le lac, bien que deux régions, près de Kelowna et à l'extrémité nord du lac, aient démontré, au cours des deux années, une plus grande abondance de plancton que les autres régions. Les crustacés sont ordinairement moins abondants près des rives qu'au large. Le volume de plancton net après sédimentation varie de 8 mm^3/cm^2 dans le lac Okanagan à 31 mm^3/cm^2 dans le lac Wood. Nous n'avons pas décelé de changements appréciables dans la composition du zooplancton, la visibilité du disque de Secchi et l'oxygène dissous de l'hypolimnion par rapport aux observations de Rawson en 1935. Cependant, les volumes de plancton net sont environ cinq fois plus grands en 1969 et trois fois plus grands en 1971 qu'en 1935. Le calcul des charges de phosphore total à partir de deux sources indépendantes aboutit aux mêmes résultats et démontre que les lacs Okanagan et Kalamalka sont encore dans les limites de l'oligotrophie, mais se rapprochent de la mésotrophie. Le lac Wood est modérément eutrophique, alors que les lacs Skaha et Osoyoos sont nettement eutrophiques, à un degré encore plus grand que le lac Washington (E.-U.) avant détournement des eaux usées, ou encore que le lac Erié. Les valeurs des déficits spatiaux de l'hypolimnion caractéristiques de lacs hautement eutrophiques confirment les estimations obtenues dans les lacs Wood, Skaha et Osoyoos. Nous exposons l'allure des changements de la charge du phosphore au cours du siècle dernier, et prédisons ce que sera cette charge en 1990, avec ou sans enlèvement de phosphore des eaux usées.

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THE increasing eutrophication of lakes in settled areas has caused some concern regarding the state of the Okanagan Valley lakes. As a result, a sampling program was set up to provide information on:

a) The vertical and horizontal distribution of temperature, oxygen, some chemical constituents, and zooplankton as a basis for planning a future, more extensive study; b) the actual trophic state of lakes Okanagan, Skaha, Osoyoos, Kalamalka, and Wood; c) the year-to-year variation of the considered parameters and the differences between the present state and those conditions 35 years ago as reported by Rawson (1939).

This information is essential for an understanding of the physical, chemical, and biological conditions existing in these lakes at present and the changes which occurred in the lakes during the last century. It also allows the predictions of future changes which might occur as a result of a fast growing human population in the valley.

Methods

Okanagan Lake was sampled on September 9–10, 1969 and August 26–27, 1971 at three points on each of 10 transects (Fig. 1). In Skaha Lake, three stations were sampled on both September 11, 1969 and August 24, 1971 representing the northern, central, and southern parts of the lake. On the same days, one station was sampled in the middle of each of the north and central basins of Osoyoos Lake. Lakes Kalamalka and Wood were sampled only once on August 25, 1971 at five and two stations, respectively. A Wisconsin type plankton net (mesh opening 77 μ) with a 25 cm diameter mouth was used at each station to obtain vertical hauls from a depth of 50 m to the surface, or from just above the bottom to the surface at stations shallower than 50 m. In addition, 0–5–m hauls were made on August 25–26, 1971 on Lake Okanagan to study the differences between inshore and offshore plankton. At each of the inshore stations, four 0–5-m vertical hauls were made perpendicularly to the shoreline spaced at 50-m intervals beginning from the point with a water depth of 5 m. One 0–5-m haul was made at each offshore station located in the middle of the west–east lake transect. Samples were taken between 0900 and 1800 hr on a sunny day with winds blowing from the south. Samples to determine the vertical distribution of plankton in Okanagan Lake were taken between 1300 and 1500 hr, on September 10, 1969, with clear sky prevailing, at transect VII, central station. Samples were collected at 5-m intervals within four separate layers 0–25, 25–50, 50–75, and 75–100 m using a transparent 6-liter van Dorn bottle. The samples within each layer were combined and filtered through a No. 20 plankton net, preserved in a 2% formaldehyde solution and analyzed using a subsampling technique with at least 200 specimens per subsample being counted. Zooplankton abundance was expressed as the number of specimens per 1 cm^2 of lake area, assuming the filtration efficiency of the net to be 100%. The counts of rotifers do not include all forms due to a loss of smaller specimens through the 77-μ mesh size netting. The plankton volume collected at each station was measured by settling in Imhoff sedimentation cones prior to specimen enumeration. In addition, at all stations, a thermistor thermometer was used to record temperature profiles to the nearest 0.1 C. At central stations, oxygen concentrations were determined using the unmodified Winkler method. Saturation values were corrected for altitude. Water samples taken from a depth of 1 m at central stations were analyzed for specific conductivity, TDS, Ca, Mg, Na, K, Cl, SO_4. Water transparency was measured using a white Secchi disc 20 cm in diameter.

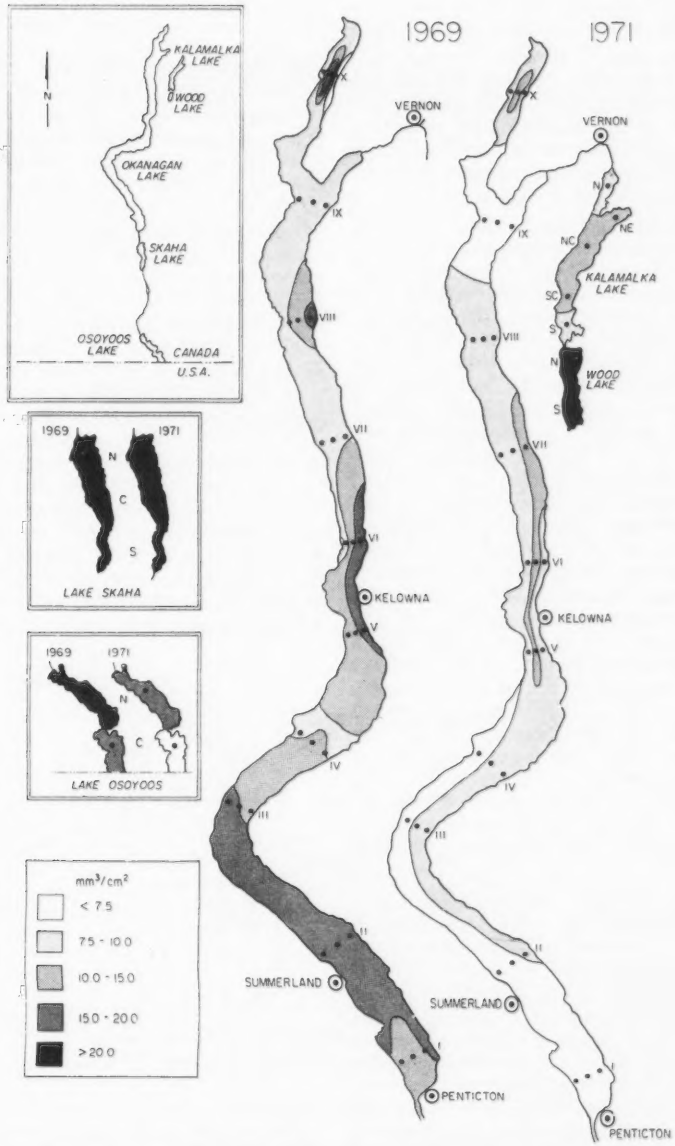

FIG. 1. Distribution of sampling stations and horizontal distribution of net plankton settled volumes in lakes Okanagan, Skaha, and Osoyoos on September 9–11, 1969, August 24–27, 1971 and in lakes Kalamalka and Wood on August 25, 1971.

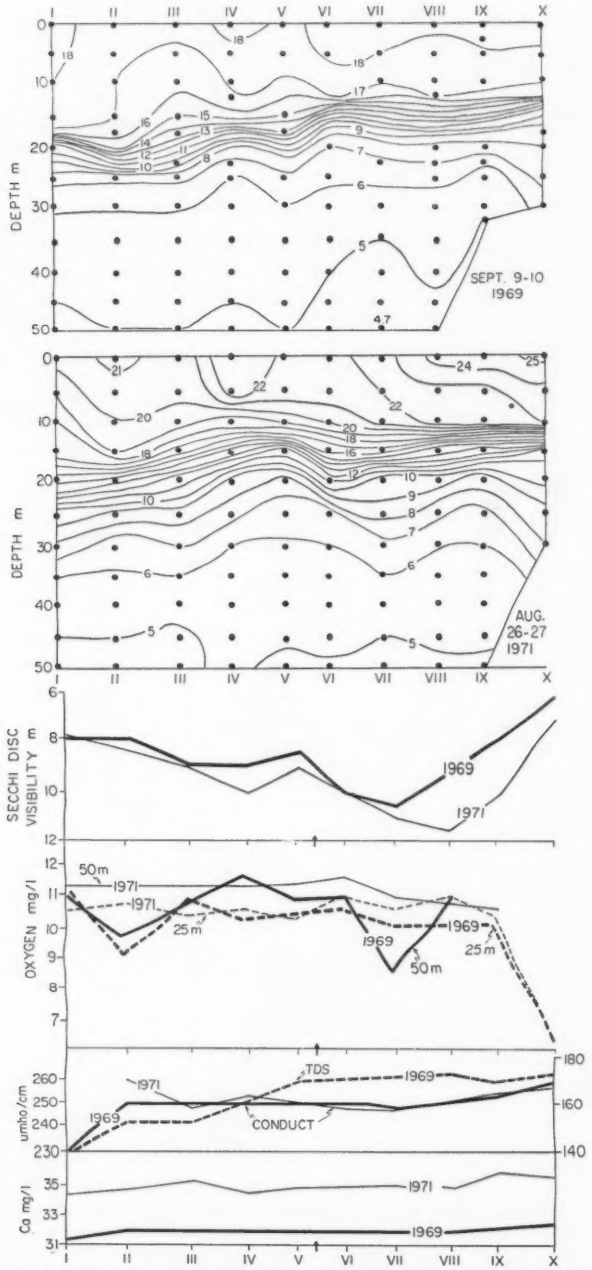

FIG. 2. Vertical and horizontal distribution of temperature (C) and horizontal distribution of Secchi disc visibility, dissolved oxygen, dissolved solids, electrical conductivity, and calcium in Lake Okanagan on September 9–11, 1969 (thick continuous and broken lines) and August 24–27, 1971 (thin continuous and broken lines). Vertical arrows indicate position of the Kelowna bridge.

Results

Limnological Characteristics

Okanagan Lake — Temperatures during the sampling period 9–10 September, 1969, followed a summer pattern of stratification, with apparent differences between the northern and southern parts (Fig. 2 and 3). The epilimnion temperature 17–19 C, extended to 12 m in the northern half of the lake while the metalimnion ranged from 12 to 20 m. The southern end, probably more exposed to the wind showed signs of the beginning of autumnal circulation since the epilimnion was slightly cooler, reaching as deep as 18 m, with the metalimnion extending from 18 to 24 m. The hypolimnetic temperatures were about 0.2 C lower in the northern part of the lake as indicated by the higher position of the 5 C isotherm. The lowest hypolimnetic temperature was found in the vicinity of the deepest part of the lake (transect VII).

A very similar pattern of thermal stratification was found on August 26–27, 1971, although the temperatures of the epilimnion were about 2–6 C higher than in 1969 due to a 2-week earlier sampling date. The epilimnion extended to 11 m at the northern end and to 16 m at the southern one or about 1–2 m less than in 1969. The bridge connecting Westside Landing with the city of Kelowna apparently affects the position of the thermocline which differs by about 3–5 m between transects V and VI situated south and north of the bridge, respectively.

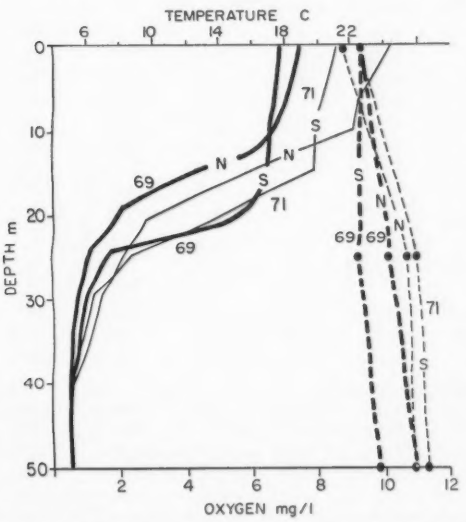

Fig. 3. Vertical distribution of temperature (continuous line) and dissolved oxygen (broken line) in northern (N) and southern (S) parts of Okanagan Lake on September 9–10, 1969 (thick line) and August 26–27, 1971 (thin line).

An apparent variation in the Secchi disc visibility was observed along the south–north axis of the lake in both years (Fig. 2): 8–8.5 m in the southern part (transects I–II); 8.5–10 m in the Peachland–Kelowna Basin (transects III–V); 9–11.5 m in the northern, deepest part (transects VI–VIII); 6–7 m in the northern end of the lake (transect X).

Dissolved oxygen was measured at 0, 25, and 50 m, the two last depths representing the upper and middle layers of the hypolimnion (Fig. 2). In September 1969, the surface waters contained from 8.4 to 9.6 mg/liter O_2, corresponding to saturation values between 94.5–109%. The degree of saturation appeared to reflect the time of day when the samples were taken, i.e. the lowest saturation values were found in the morning, whereas the highest ones occurred during the late afternoon. The hypolimnetic waters contained from 6.4 to 11.7 mg/liter O_2 (56–98% of saturation). The lowest value, 6.4 mg/liter O_2, was found at the northernmost transect X, close to the bottom near 30 m. The second lowest value, 8.7 mg/liter O_2, appeared at the 50 m depth at transect VII, concurrently with the lowest water temperature 4.7 C. This might indicate that spring overturn was not quite as effective in mixing the deeper water of this part of the lake as it was in the shallower stations. The average value of the dissolved oxygen content in the hypolimnion (25–50 m) for the whole lake was 10.5 mg/liter O_2, corresponding to 88% of saturation. Similar ranges of values were found on August 26–27, 1971. The hypolimnetic waters (25–50 m) contained between 6.4–11.6 mg/liter O_2 (59–99% of saturation) with a lake average of 10.7 mg/liter (91% saturation). The differences between particular transects were smaller than in 1969.

The major ions were relatively uniformly distributed throughout the lake, although certain north–south trends could be observed in some of them (Table 1, Fig. 2). In September 1969, specific conductivity ranged from 231 µmho/cm at the south end of the lake to 259 µmho/cm at the north end. In the main body of water the most characteristic value was 250 µmho/cm which is very close to the lakes' average values of 251 µmho/cm in 1969 and 252 µmho/cm in 1971. A similar tendency could be seen in the distribution of total dissolved solids (TDS) which ranged from 141 mg/liter at the south end to 174 mg/liter in the north basin, with a 1969 lake average of 164 mg/liter. Also, calcium was higher in 1969 at the north end, reaching 32.5 mg/liter Ca as compared with 31.4 mg/liter Ca at the south end with a lake average of 31.9 mg/liter Ca.

TABLE 1. Chemical analysis of water from lakes Okanagan, Skaha, Osoyoos, Wood, and Kalamalka. Samples taken at 1 m depth.

Transect station	Date	Spec. conductivity μmho/cm	TDS	Ca	Mg	Na	K	Chloride Cl	Sulphate SO_4
			mg/liter						
				Okanagan					
I	Sept. 9, '69	231	141	31.4	9.2	8.4	2.3	2.4	21
II	"	250	152	31.9	9.2	8.3	2.3	1.3	24
III	"	250	153	31.9	9.1	8.3	2.3	2.0	26
IV	"	250	162	31.9	9.1	8.4	2.3	1.5	21
V	"	250	169	31.9	9.1	8.5	2.2	1.5	19
VI	Sept. 10, '69	250	172	31.9	9.1	8.4	2.3	1.9	23
VII	"	248	173	31.9	9.1	8.3	2.3	1.6	26
VIII	"	250	174	31.9	9.2	8.3	2.3	1.5	25
IX	"	253	170	32.2	9.2	8.4	2.3	2.0	27
X	"	259	173	32.5	9.7	8.2	2.2	1.6	26
Lake avg		251	164	31.9	9.2	8.4	2.3	1.7	24
I	Aug. 8, '71	–	–	34.5	9.9	9.0	2.4	2.0	25
II	"	260	–	34.8	9.5	8.9	2.4	2.0	25
III	"	248	–	35.3	9.5	8.4	2.4	2.0	24
IV	"	253	–	34.6	9.6	8.3	2.4	2.0	24
V	"	250	–	34.9	9.5	8.3	2.4	1.0	23
VI	Aug. 26, '71	248	–	35.0	9.5	8.4	2.4	1.0	24
VII	"	247	–	35.1	9.5	8.5	2.4	1.0	23
VIII	"	250	–	34.9	9.6	8.5	2.4	1.0	24
IX	"	253	–	35.9	9.7	8.7	2.5	1.0	24
X	"	257	–	35.7	10.1	8.9	2.7	1.0	22
Lake avg		252	–	35.1	9.6	8.6	2.4	1.4	24
				Skaha					
N(orth)	Sept. 9, '69	249	165	31.1	9.1	8.6	2.3	1.9	23
C(entral)	"	250	164	31.4	9.2	8.6	2.3	1.6	28
S(outh)	"	250	164	31.4	9.2	8.6	2.3	2.4	26
Lake avg	"	250	164	31.3	9.2	8.6	2.3	2.0	26
N	Aug. 24, '71	246	–	33.6	9.4	8.8	2.3	1.0	23
C	"	243	–	34.2	9.5	8.9	2.4	1.0	20
S	"	245	–	33.5	9.5	8.7	2.4	2.0	21
Lake avg	"	245	–	33.8	9.5	8.8	2.4	1.3	21
				Osoyoos					
N	Sept. 11, '69	252	168	31.6	9.7	9.0	2.4	1.6	25
C	"	251	169	31.4	9.7	9.0	2.4	1.6	26
Lake avg	"	251	168	31.5	9.7	9.0	2.4	1.6	25
N	Aug. 8, '71	249	–	33.2	9.6	9.0	2.4	2.0	19
C	"	251	–	33.5	9.7	9.0	2.4	1.0	23
Lake avg	"	250	–	33.3	9.7	9.0	2.4	1.5	21
				Kalamalka					
N	Aug. 25, '71	375	243	37.8	19.9	15.8	5.0	2.0	44
N C	"	370	250	38.5	20.0	15.5	5.1	2.0	44
S C	"	368	261	36.1	20.3	15.5	5.1	2.0	50
S	"	362	253	37.0	20.3	15.3	5.0	1.0	46
Lake avg	"	369	252	37.3	20.1	15.5	5.0	1.7	46
				Wood					
N	Aug. 25, '71	294	224	22.1	20.6	18.4	4.6	3.0	26
S	"	296	199	21.5	20.8	18.4	4.6	3.0	25
Lake avg	"	295	211	21.8	20.7	18.4	4.6	3.0	25

Though in August 1971 the calcium concentration was on the average 3.2 mg/liter Ca higher than in 1969, the same tendency of decreasing values from north to south was apparent. The remaining ions were either distributed rather uniformly throughout the lake or did not show any consistent trends in their horizontal distribution. The lake average concentrations were very similar in September 1969 and August 1971: magnesium 9.2 and 9.6 mg/liter Mg, sodium 8.4 and 8.6 mg/liter Na, potassium 2.3 and 2.4 mg/liter K, chloride 1.7 and 1.4 mg/liter Cl, and sulphate 2.4 and 2.4 mg/liter SO_4, respectively.

Skaha Lake — The temperature curve of Skaha Lake in September 1969 very closely resembles that of the northern part of Okanagan Lake (Fig. 4). The mean epilimnion temperatures varied from 17.6 in the north to 18.4 C in the south. The epilimnion extended to a depth of 10 m in the north and to about 12 m in the south. Generally, both the epi- and hypolimnion of the southern part were about 0.7 C warmer than those of the northern one. A much greater variation was found in the depth of the epilimnion on August 24, 1971 than on September 11, 1969. Due to a strong wind blowing from the south, the epilimnion reached a depth of 12.5 m at the north end, 9 m at the center, and 6 m at the south end of the lake. Also, the temperature of the epilimnion was up to 4 C higher and that of hypolimnion up to 2 C higher than on September 11, 1969.

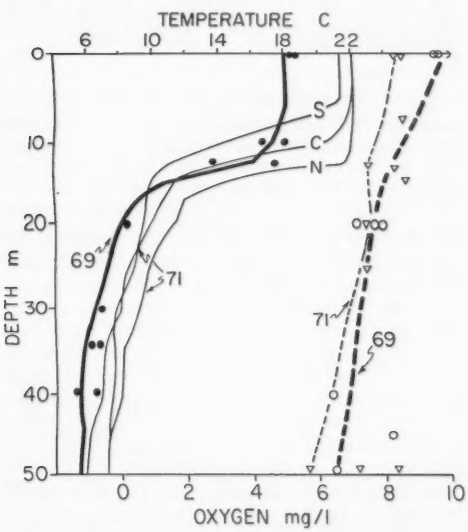

FIG. 4. Vertical distribution of temperature (continuous lines) and dissolved oxygen (broken lines) in Lake Skaha on September 11, 1969 (thick lines) and August 24, 1971 (thin lines). Oxygen curves are drawn for central station only; open circles and triangles denote oxygen values in remaining stations in September 1969 and August 1971, respectively. The temperature curve for September 1969 refers to the central station; black dots indicate range of temperature in remaining stations. Three curves are drawn for August 1971 separately for southern (S), central (C), and northern (N) stations.

Oxygen concentrations in the hypolimnion on September 11, 1969 ranged from 6.3 mg/liter O_2 in the southern basin to 8.1 mg/liter O_2 in the northern one (Fig. 4). A similar range was found on August 24, 1971–from 5.8 mg/liter O_2 in the central station to 8.4 mg/liter O_2 in the northern one.

Secchi disc visibility varied from 2.5 to 2.8 m in September 1969 but was almost twice higher in August 1971, i.e. from 5.0 to 5.4 m.

The major ions were rather uniformly distributed at all stations sampled with values similar to those in Okanagan Lake (Table 1).

Osoyoos Lake — On September 11, 1969 the mean epilimnion temperature of the north basin was 19 C and of the central basin 19.5 C, about 0.6–1.9 C higher than in Skaha Lake. Similarly, on August 24, 1971 Osoyoos Lake displayed a 0.5 C higher epilimnion temperature than Skaha Lake. This is probably because 1) Skaha Lake receives its water from larger and slightly colder Okanagan Lake; 2) before entering Osoyoos Lake, water can be warmed in shallow Vaseaux Lake situated between Skaha and Osoyoos lakes; 3) mean summer air temperatures are about 2.5 C higher in Osoyoos than in Penticton (Kelley and Spilsbury 1949). The hypolimnion of the shallower, central part of Osoyoos Lake was 1.8–2 C warmer than that in the deeper, northern part, both in September 1969 and August 1971.

Dissolved oxygen values from near bottom water in the central part of Osoyoos Lake were 0.8 mg/liter O_2 in September 1969 and 0.15 mg/liter O_2 in August 1971 (Fig. 5). More oxygen was found in the northern part: 3.6 mg/liter O_2 in September 1969 and 4.5 mg/liter O_2 in August 1971.

The Secchi disc visibility extended to 4.1 m in September 1969. Comparable values of between 3.5–4.5 m (in average 4.0 m) were found in August 1971.

The major ions at the surface of Osoyoos Lake differed from that of Skaha and Okanagan lakes only in the slightly higher amounts of magnesium and sodium (Table 1).

Kalamalka Lake — On August 25, 1971 the epilimnion extended to about 10 m depth with a mean temperature at the central station of 22.9 C. Very

low temperatures were found in the hypolimnion with 4.1–4.5 C at the 50 m depth. No significant differences were revealed in the temperatures at different stations. The general stratification pattern resembled that of the north of Lake Okanagan and the central station of Lake Skaha, the only exception being an apparently colder hypolimnion in Lake Kalamalka than in lakes Okanagan and Skaha.

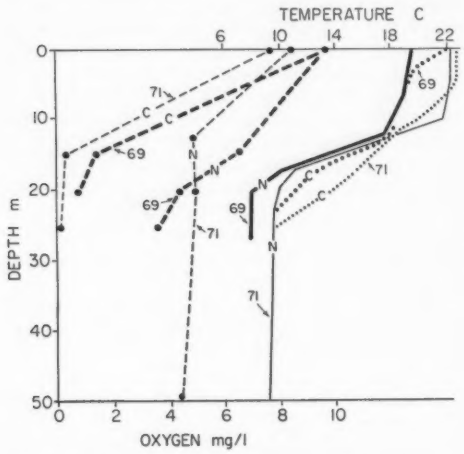

FIG. 5. Vertical distribution of temperature (continuous and dotted lines) and oxygen (broken line) in the central (C) and northern (N) parts of Lake Osoyoos on September 9, 1969 and August 24, 1971.

The dissolved oxygen content was very high in Lake Kalamalka and at 50 m reached between 10.4–11.9 mg/liter O_2 corresponding to an average of 94% of saturation (Fig. 6).

Secchi disc transparency was 5.5–6 m, 5.7 m on average. The major ion contents were apparently higher than in the previously described lakes. Specific conductivity ranged from 362 µmho/cm at the south end of the lake to 375 µmho/cm at the north end, with a lake average of 369 µmho/cm. Also, calcium contents were higher in the northern half of the lake, 37.8–38.5 mg/liter Ca, than in the southern end, 36.1–37 mg/liter Ca, (average 37.3 mg/liter Ca). The remaining ions did not show any significant horizontal variation. The mean content of magnesium was 20.1 mg/liter Mg, sodium 15.5 mg/liter Na, potassium 5 mg/liter K, chloride 1.7 mg/liter Cl, sulphate 46 mg/liter SO_4, and TDS 252 mg/liter; values about twice as high as those in lakes Okanagan, Skaha, and Osoyoos (Table 1).

Wood Lake — On August 25, 1971 the epilimnion extended down to about 5 m depth with a mean temperature of 22.5 C. A very thick layer of metalimnion between 5–20 m had a mean gradient of 1.3 C/m. Also, the hypolimnetic temperature was relatively low, between 5.7–6.6 C. Dissolved oxygen was very low near the bottom, ranging from 0.3 to 0.9 mg/liter O_2 (2.5–8% of saturation) (Fig. 7). Secchi disc transparency was 3.8–4 m.

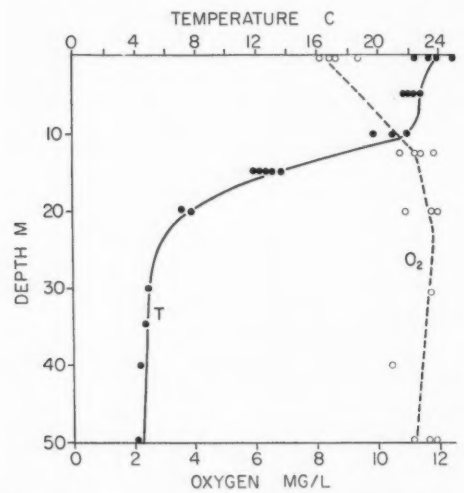

FIG. 6. Vertical distribution of temperature (continuous line) and dissolved oxygen (broken line) in Lake Kalamalka on August 25, 1971. Curves refer to the central station; horizontal dots and open circles indicate ranges of values in other stations.

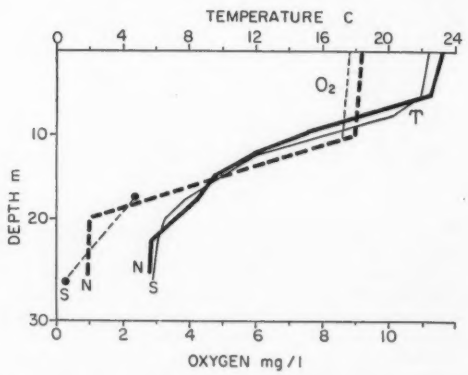

FIG. 7. Vertical distribution of temperature (continuous line) and dissolved oxygen (broken line) in northern (N) and southern (S) parts of Wood Lake on August 25, 1971.

In spite of the close proximity of Lake Kalamalka, the water of Wood Lake differed in chemical composition from the former. Only 21.8 mg/liter Ca and 25 mg/liter SO_4 on the average was encountered in Wood Lake, or about half of that occurring in Lake Kalamalka. The concentrations of magnesium 20.7 mg/liter Mg, sodium 18.4 mg/liter Na, and chloride 3.0 mg/liter Cl were apparently higher than in Lake Kalamalka and were the highest within the whole group of lakes under study (Table 1).

Crustacean Plankton.

Okanagan Lake — In total, 13 species were found in the Okanagan Valley lakes and all of them were present in Okanagan Lake (Table 2). Of four copepod species, *Cyclops bicuspidatus thomasi* and *Diaptomus ashlandi* were the most abundant, contributing to about 60 and 30%, respectively, of the total number of plankters. *Epischura nevadensis* was widespread but low in number, in average 0.4–1.3%. *Cyclops vernalis* was found only once in very low numbers. Of nine cladoceran species, *Daphnia thorata* was the most abundant, but its contribution to the total number of crustaceans was not greater than 1–1.3%. The second most abundant cladoceran was *Daphnia longiremis* with a frequency of occurrence of 0.2–1%. The remaining species, *Bosmina longirostris*, *Bosmina coregoni longispina*, *Diaphanosoma leuchtenbergianum*, and *Leptodora kindtii* were very low in number, as a rule less than 0.3% of the total. Only single specimens of *Daphnia pulex*, *Daphnia schoedleri* (× *pulex*) and *Sida crystallina* were found in August, 1971. There were no significant differences in percentage species composition between both years of investigation.

Based on the vertical series taken on September 10, 1969, it was found that most species were distributed in the uppermost 25-m layer (Fig. 8). The most abundant species, *D. ashlandi* and *C. bicuspidatus thomasi* were distributed throughout the 0–50-m layer with a maximum density in the upper 25-m layer. The only exceptions were the nauplii of *C. bicuspidatus thomasi* which showed a maximum density in the 25–50-m layer. Also, a few *D. longiremis* were found below the 50 m depth. Eighty-nine percent of the total plankters were located above 50 m.

The pattern of the horizontal distribution of the total number of planktonic crustaceans in Lake Okanagan is presented in Fig. 9. In September 1969, the plankton was distributed more or less uniformly through the central and most of the northern part of the lake with densities between 150 and 200 individuals/cm^2. The lowest amount at the eastern station of transect X is explained by shallow depth at this station. A significantly higher number of plankters (250–350 individuals/cm^2) was found at the southern end of the lake, transects II and III. In August 1971, the general pattern of distribution was similarly uniform but the densities of plankters were about half of those in September 1969, and no significantly greater densities were found in the southern basin. A pattern of the horizontal distribution of plankton measured as the settled volume in mm^3/cm^2 of lake surface is shown in Fig. 1. The highest plankton volumes were found in September 1969 in the southern basin (transects I/III) with 14–20 mm^3/cm^2, in the vicinity of Kelowna (transects V/VII with 9–17 mm^3/cm^2 and in the most northern basin (transect X) with 21 mm^3/cm^2. In most of the remaining lake area, the volume of plankton amounted to 5–11 mm^3/cm^2. The high volume of plankton in the southern basin was mainly due to the highest density of copepodids of *C. bicuspidatus thomasi* and *D. ashlandi*. Also, *E. nevadensis*, *B. longirostris*, *B. coregoni longispina*, and *L. kindtii* were more abundant in the southern basin. Although the settled volume of plankton was lower in August 1971, with 8.1 mm^3/cm^2 in average, the two areas of maximum 1971 amount (10–13 mm^3/cm^2) were again located in the vicinity of Kelowna and in the most northern basin. No above average volumes were found in the southern basin as in September 1969. All species (except those encountered sporadically in very low numbers) were distributed all over the lake (Fig. 10). The coefficient of variation of the abundances in particular stations, expressed as the ratio of standard deviation to the lake mean density, was between 0.20–0.40 for more abundant species and between 0.40–1.5 for less abundant ones. Within these limits, statistically significant differences were found in the densities of some species in different parts of the lake. In September 1969, copepodids of *D. ashlandi* and *C. bicuspidatus thomasi*, *E. nevadensis*, *B. longirostris*, *B. coregoni longispina*, *D. leuchtenbergianum*, and *L. kindtii* were more abundant in the southern basin than in the remaining parts of the lake. In August 1971, the highest number of *C. bicuspidatus thomasi* and *D. ashlandi* copepodids were found in the central part of the lake. In both 1969 and 1971, the apparently higher number of adults and the lower number of copepodids in the northern end of the lake indicated a more advanced stage of the population development there. Also, in September 1969, the mean size of *D. longiremis* (Fig. 11) was significantly higher in the northern part (1254 μ) than in the southern one (1088 μ). The corresponding values of the north and south end for August 1971 (Fig. 12), were 1170 μ and 1016 μ, respectively. The greater mean size of *Daphnia* in 1969 could well be the result of more adults

TABLE 2. Species composition of crustaean plankton (individuals per cm²) in Lake Okanagan, September 9–10, 1969, and August 624–2, 1971 (*italics*).

Transect	Station	Depth	*Epischura nevadensis* Lilljeborg	*Diaptomus ashlandi* Marsh			*Cyclops bicuspidatus thomasi* Forbes			*Cyclops vernalis* Fischer	*Daphnia thorata* Forbes	*Daphnia longiremis* Sars	*Daphnia schoedleri* Sars (× *pulex*?)	*Daphnia pulex* Leydig	*Bosmina longirostris* (O. F. Müller)	*Bosmina coregoni longispina* Leydig	*Diaphanosoma leuchtenbergianum* Fischer	*Leptodora kindtii* (Focke)	*Sida crystallina* (O. F. Müller)	Total
				adult	copepodid	nauplius	adult	copepodid	nauplius											
I	W	50	0.6	–	69.3	0.8	–	47.7	125.5	–	2.0	0.2	–	–	0.4	0.2	0.4	<0.1	–	247.1
		50	*0.9*	–	*20.1*	*0.8*	–	*10.5*	*44.1*	–	*1.6*	*1.2*	–	–	*<0.1*	*<0.1*	*0.4*	–	–	*79.6*
	C	50	0.3	–	70.7	0.8	–	31.5	32.3	–	0.2	0.1	–	–	0.6	0.2	0.6	<0.1	–	137.3
		50	*2.2*	–	*20.1*	*0.4*	–	*16.6*	*49.5*	–	*0.8*	*0.8*	–	–	*<0.1*	*<0.1*	*<0.1*	*<0.1*	–	*90.6*
	E	29	0.8	–	70.1	–	–	23.9	135.5	–	1.8	0.5	–	–	0.6	<0.1	0.6	–	–	233.8
		50	*1.0*	–	*23.6*	*0.8*	–	*16.6*	*43.0*	–	*1.9*	*0.9*	–	–	*0.8*	*<0.1*	*0.4*	–	–	*88.9*
II	W	35	0.1	0.8	96.2	0.8	1.5	49.2	66.9	–	4.7	0.7	–	–	0.3	0.1	0.3	–	–	221.6
		15	*0.6*	–	*7.8*	*0.7*	–	*3.3*	*0.2*	–	*0.7*	–	–	–	*<0.1*	*<0.1*	*0.2*	–	–	*13.6*
	C	50	1.0	1.5	109.2	–	1.5	32.4	183.0	–	0.5	0.3	–	–	1.9	0.1	0.3	–	–	331.7
		50	*2.2*	*1.6*	*25.5*	–	–	*16.1*	*78.0*	–	*2.9*	*0.7*	–	–	*<0.1*	*<0.1*	–	*<0.1*	–	*128.6*
	E	27	0.7	–	108.5	–	–	54.5	38.5	–	3.8	0.2	–	–	0.6	0.1	0.3	0.1	–	207.4
		50	*4.0*	*0.5*	*33.3*	*3.1*	–	*20.1*	*57.2*	–	*2.1*	*1.0*	–	–	*<0.1*	*0.3*	*0.5*	*<0.1*	–	*123.5*
III	W	50	1.4	–	94.0	–	–	55.4	117.0	–	2.6	0.3	–	–	0.8	0.2	1.4	.1	–	273.2
		50	*0.2*	*0.5*	*30.2*	*1.6*	*0.5*	*23.9*	*60.8*	–	*2.1*	*2.1*	–	–	*<0.1*	*<0.1*	*<0.1*	*<0.1*	–	*122.5*
	C	50	0.2	–	106.0	–	–	44.7	148.0	–	3.3	0.8	–	–	0.8	1.2	0.2	1.0	–	306.2
		50	*1.2*	–	*41.1*	*1.0*	–	*18.2*	*56.7*	–	*0.5*	*3.1*	–	–	*0.1*	*0.1*	–	*<0.1*	–	*122.1*
	E	39	1.0	–	95.5	–	–	34.6	81.5	–	1.6	0.1	–	–	0.9	0.3	0.4	–	–	215.9
		50	*0.8*	*0.5*	*33.8*	*1.6*	–	*16.6*	*52.0*	–	*1.6*	*1.6*	–	–	*<0.1*	*<0.1*	–	–	–	*109.1*
IV	W	50	1.2	–	65.2	0.8	–	19.2	74.7	–	2.3	0.2	–	–	1.0	0.2	0.6	–	–	165.4
		41	*1.4*	–	*17.1*	*2.5*	*0.3*	*15.5*	*20.8*	–	*0.6*	*0.6*	–	–	*0.4*	*<0.1*	*<0.1*	*<0.1*	–	*59.3*
	C	50	0.6	0.8	46.2	–	–	25.4	148.0	–	1.5	0.3	–	–	0.8	0.1	0.2	–	–	223.9
		50	*1.3*	*0.5*	*20.3*	*1.0*	–	*21.8*	*84.8*	–	*2.6*	*0.5*	–	–	*<0.1*	*<0.1*	*0.1*	*<0.1*	–	*133.7*
	E	50	1.2	0.8	51.5	–	–	25.4	94.0	–	2.6	1.1	–	–	0.2	0.4	–	.4	–	177.6
		50	*2.4*	–	*29.6*	*1.6*	–	*23.4*	*56.2*	–	*0.5*	*5.2*	–	–	*<0.1*	*<0.1*	*<0.1*	*<0.1*	–	*119.0*
V	W	26	0.8	–	71.0	–	–	22.2	12.3	–	3.6	<0.1	–	–	0.7	<0.1	0.2	–	–	110.8
		34	*1.3*	–	*27.1*	*2.7*	*0.4*	*22.5*	*26.7*	–	*3.1*	*1.6*	–	–	*0.3*	–	*0.2*	*<0.1*	–	*85.9*
	C	50	1.0	–	80.0	–	–	31.5	56.9	–	2.7	0.1	–	–	0.6	0.3	0.2	–	–	173.3
		50	*1.2*	*0.5*	*35.9*	*0.5*	–	*35.4*	*48.4*	–	*2.6*	*2.6*	*<0.1*	–	*0.2*	*0.3*	*1.0*	*<0.1*	–	*129.2*
	E	37	1.3	–	108.5	–	–	40.0	32.3	–	1.9	<0.1	–	–	0.6	0.1	0.3	–	–	185.0
		50	*1.5*	–	*36.8*	*2.6*	*1.2*	*24.4*	*20.1*	–	*0.4*	*0.4*	–	–	*0.4*	*<0.1*	*<0.1*	–	–	*87.5*
VI	W	50	0.5	0.8	49.2	1.5	1.5	19.2	97.8	–	1.5	0.2	–	–	0.5	0.1	0.2	–	–	173.0
		50	*1.7*	–	*33.3*	*4.7*	*1.6*	*22.9*	*43.2*	*0.52*	*1.8*	*2.9*	–	–	*0.4*	*0.3*	*<0.1*	*<0.1*	–	*113.3*
	C	50	0.5	–	61.5	–	0.8	20.7	126.6	–	1.8	0.3	–	–	0.2	–	0.5	–	–	212.8
		50	*0.2*	–	*35.6*	*3.9*	*0.5*	*37.9*	*59.6*	–	*0.8*	*1.6*	–	–	*0.4*	*0.1*	*0.4*	*<0.1*	–	*140.6*
	E	46	0.5	–	78.5	–	–	43.0	75.5	–	2.3	1.8	–	–	1.0	0.3	0.2	–	–	203.1
		50	*0.3*	*0.4*	*38.7*	*0.4*	–	*16.3*	*14.3*	–	*3.1*	*0.8*	–	–	*0.4*	*0.1*	*<0.1*	–	–	*83.1*
VII	W	50	0.1	1.5	36.1	–	–	31.5	90.8	–	1.0	0.2	–	–	0.7	0.1	<0.1	–	–	162.0
		50	*3.2*	–	*38.7*	*1.6*	–	*29.4*	*81.3*	–	*3.1*	*0.8*	–	–	*<0.1*	*0.2*	*0.5*	*<0.1*	–	*158.8*
	C	50	0.5	0.8	47.8	–	1.5	20.0	99.1	–	0.7	<0.1	–	–	0.9	0.2	0.4	–	–	171.9
		50	*2.2*	–	*30.7*	*1.6*	–	*21.3*	*72.3*	–	*1.3*	*1.2*	–	–	*<0.1*	*0.3*	*0.3*	–	–	*131.3*
	E	50	0.8	1.5	51.5	–	–	26.2	84.5	–	0.7	0.4	–	–	1.0	–	0.3	–	–	166.9
		50	*1.9*	–	*33.8*	*1.0*	*0.5*	*32.2*	*58.8*	–	*0.5*	*1.0*	–	–	*0.9*	*0.6*	*0.1*	*<0.1*	–	*131.5*
VIII	W	50	0.1	–	53.1	–	–	21.5	124.5	–	1.7	0.5	–	–	0.5	0.1	0.3	–	–	202.3
		50	*1.3*	–	*45.2*	*3.1*	*0.5*	*22.9*	*47.3*	–	*1.5*	–	–	–	*0.2*	*<0.1*	*0.5*	–	–	*122.6*
	C	50	0.3	1.5	69.2	1.5	0.8	26.2	87.5	–	1.8	0.2	–	–	0.4	<0.1	0.4	–	–	189.8
		50	*0.1*	*0.5*	*38.0*	*1.0*	*0.5*	*19.2*	*54.6*	–	*1.0*	*0.5*	–	–	*0.4*	*<0.1*	*0.7*	–	–	*117.1*
	E	28	1.3	1.5	124.5	–	–	31.5	46.9	–	2.2	0.2	–	–	1.0	0.3	0.4	–	–	209.8
		50	*1.1*	–	*36.4*	–	–	*20.8*	*66.0*	–	*1.0*	–	–	–	*0.6*	*<0.1*	*<0.1*	–	–	*126.0*
IX	W	34	0.8	2.3	53.8	<0.1	–	17.7	82.5	–	0.6	0.2	–	–	1.0	<0.1	0.3	0.1	–	159.3
		50	*0.4*	*0.8*	*33.0*	*1.6*	*0.8*	*19.7*	*32.1*	–	–	–	–	–	*0.2*	*<0.1*	*0.5*	–	–	*89.1*
	C	30	1.0	1.5	49.3	–	–	37.0	76.2	–	0.9	0.1	–	–	<0.1	–	0.9	–	–	166.9
		50	*1.2*	–	*20.9*	*0.8*	*0.4*	*17.0*	*36.0*	–	*0.8*	–	–	–	*0.2*	*<0.1*	*0.2*	–	–	*77.5*
	E	22	0.6	2.1	72.0	–	–	23.1	15.4	–	2.0	<0.1	–	–	0.3	0.1	0.1	–	–	115.7
		25	*0.4*	–	*28.1*	*0.5*	*0.3*	*14.0*	*11.4*	–	*1.2*	*0.4*	–	–	*<0.1*	–	*0.3*	*<0.1*	–	*56.7*
X	W	19	1.1	2.3	67.2	0.8	–	16.5	2.3	–	2.1	<0.1	–	–	–	–	0.3	–	–	92.6
		25	*1.3*	*0.3*	*18.6*	*2.2*	*0.6*	*26.4*	*9.6*	–	–	–	–	–	*0.3*	–	*0.7*	*<0.1*	–	*67.9*
	C	30	0.4	–	57.7	0.8	3.9	45.4	50.0	–	0.4	0.1	–	–	–	<0.1	0.4	–	–	159.1
		30	*1.2*	*0.8*	*26.3*	*1.6*	*1.2*	*38.7*	*29.0*	–	*1.9*	–	–	–	*0.8*	–	*0.6*	*<0.1*	–	*102.8*
	E	12	0.8	0.8	32.4	0.5	–	8.5	1.1	–	1.5	–	–	–	<0.1	–	0.7	–	–	46.4
		12	*1.3*	*0.2*	*12.9*	*0.2*	–	*0.9*	*0.8*	–	*0.7*	–	–	*<.01*	*0.4*	*<0.1*	*0.7*	–	*<0.1*	*18.3*
Lake avg ind./cm²			0.7	0.7	71.5	0.3	0.4	30.9	80.2	–	1.8	0.3	–	–	0.6	0.2	0.4	0.1	–	188.1
			1.3	*0.2*	*29.1*	*1.5*	*0.3*	*20.8*	*43.8*	*<0.1*	*1.3*	*1.0*	*< .01*	*<0.1*	*0.3*	*<0.1*	*0.3*	*<0.1*	*<0.1*	*100.9*
%			0.4	0.4	38.0	0.2	0.2	16.4	42.5	–	1.0	0.2	–	–	0.3	0.1	0.2	<0.1	–	100.0
			1.3	*0.2*	*29.0*	*1.5*	*0.3*	*20.8*	*43.7*	–	*1.3*	*1.0*	*< .01*	–	*0.3*	*0.1*	*0.3*	*<0.1*	*<0.1*	*100.0*

in the population or as in Fig. 11 due to a higher growth rate. The fact that in both years *Daphnia* were characterized by a significantly larger size upon attainment of maturity could be interpreted that a higher growth rate occurred. All differences were statistically significant at $P<0.05$.

The differences between the plankton densities in the 0–5-m layer within inshore and offshore waters are presented in Table 3. The concentration of planktonic crustaceans in the inshore waters was, on the average, only 50% of that in the offshore waters. The ratio of offshore to inshore concentrations provides information on the tendency of species to occupy particular zones. Copepodids of *D. ashlandi*, *D. leuchtenbergianum*, and *C. bicuspidatus thomasi* displayed the greatest offshore tendency, being 2.8–2.2 times more abundant offshore than inshore. Nauplii of *D. ashlandi* and *B. longiros-*

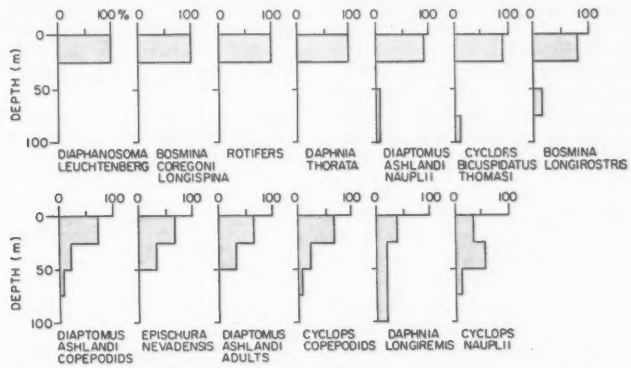

FIG. 8. Vertical distribution of zooplankton in Lake Okanagan (September 10, 1969; 1300–1500 hr, central part, transect VII).

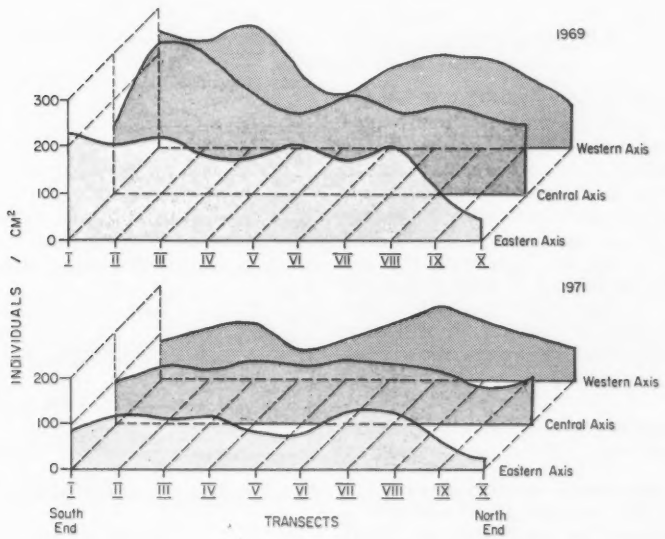

FIG. 9. Horizontal distribution of crustacean plankton along three axes of Lake Okanagan on September 9–10, 1969, (*upper*) and on August 26–27, 1971 (*lower*).

tris were found in both zones in similar densities. The remaining species were 1.6–1.9 times more abundant in offshore waters.

Lake Skaha — No significant difference in the composition of species and their numerical proportions was found between Lake Skaha (Table 4) and Lake Okanagan (Table 2). Of Lake Okanagan's 13 species, as many as 12 were present in Lake Skaha with *C. bicuspidatus thomasi* representing, in 1969, 45% and *D. ashlandi* 50% of the total crustacean number. In 1971, figures were 65 and 30% respectively. The cladocerans contributed 2.7% in 1969 and 4.3% in 1971 to the total individual number with *D. leuchtenbergianum* (0.9 and 2.2%) and *D. longiremis* (1.2 and 0.9%) being the most abundant. A significant difference was found in the population structure of *D. ashlandi*. Nineteen and 15% of the population consisted of adults in Lake Skaha while only 1 and 0.7% were adults in the population in Okanagan Lake. Correspondingly, very few *D. ashlandi* nauplii were found in Okanagan Lake (0.6 and 4.9%) while in Lake Skaha 34 and 48% of the population was in the nauplial stage. Also, more adults of *C. bicuspidatus thomasi* were found in Lake Skaha (10.5 and 1.7%) as compared with Okanagan Lake (0.3 and 0.4%). Thus, the higher settled plankton volumes encountered in Lake Skaha can be explained in part by structural differences and not exclusively by differences in numbers of animals between the two lakes.

Lake Osoyoos — The crustacean plankton of Lake Osoyoos closely resembles that of Lake Skaha,

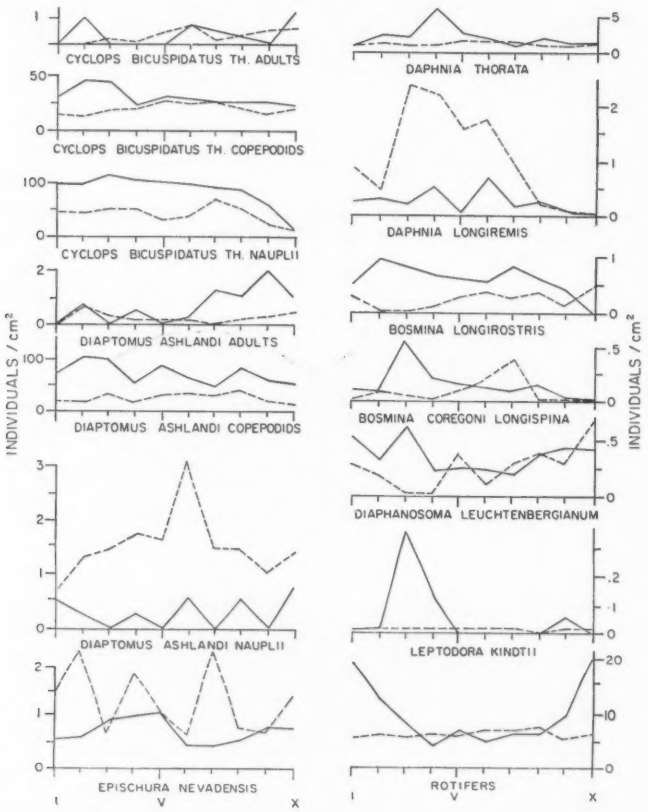

FIG. 10. Horizontal distribution of particular species of zooplankton in Lake Okanagan, September 9–10, 1969, (continuous line) and on August 26–27, 1971 (broken line).

both in species composition and in the structure of the *C. bicuspidatus thomasi* and *D. ashlandi* populations (Table 4). The absence of *B. coregoni longispina*

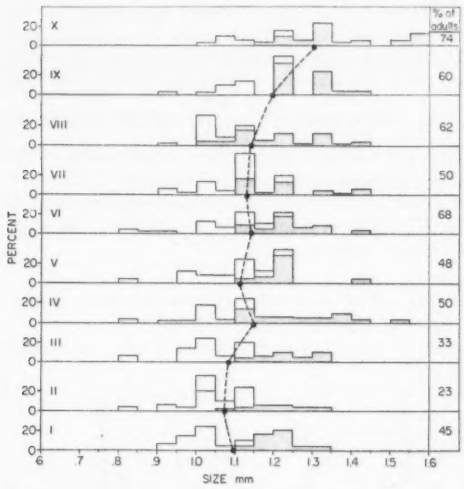

FIG. 11. Size structure of the population of *Daphnia longiremis* in different transects of Lake Okanagan, September 9–10, 1969. Shaded area denotes adult specimens, unshaded — juveniles. Dots interconnected with dashed line denote average size (head + valve) of animals.

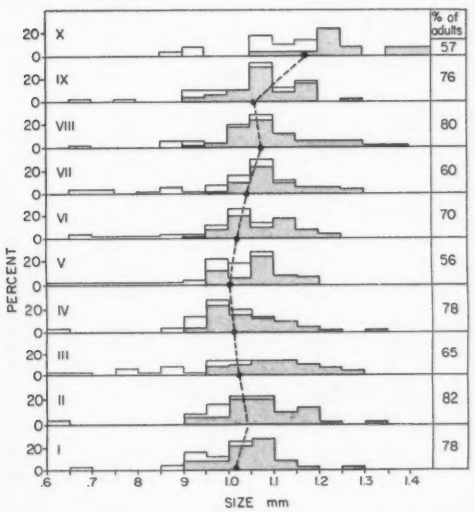

FIG. 12. Size structure of the population of *Daphnia longiremis* in different transects of Lake Okanagan, August 24–27, 1971. Explanations as in Fig. 11.

and the slightly higher percentage of *D. leuchtenbergianum* are the only apparent differences. However, the total number of animals, amounting to 161 individuals/cm² in September 1969 and only 76 individuals/cm² in August 1971, was lower than that of Lake Skaha and even that of Okanagan Lake. The corresponding settled volumes of plankton were relatively higher, 25.9 and 10.9 mm³/cm² in 1969 and 1971, respectively, being related to the high percentage of copepodids and adults in the populations of *C. bicuspidatus thomasi* and *D. ashlandi*.

Lake Kalamalka — Nine species were found in Lake Kalamalka (Table 4), with *C. bicuspidatus thomasi* (56.3%) and *D. ashlandi* (31.3%) most abundant. Very few *C. bicuspidatus thomasi* adults were found in spite of a quite high percentage of cyclopoid nauplii. Ninety-eight percent of the population of *D. ashlandi* was composed of copepodids. No adults were found. The age structure of the two dominant species closely resembled the Okanagan Lake situation. However, cladocerans were more frequent in Lake Kalamalka, contributing to 9.3% of the total number of crustaceans as compared with 3.2% in Okanagan Lake. *D. longiremis* was the most abundant cladoceran with 6.3%. Crustacean distribution throughout the lake was rather uniform ranging from 101 to 169 individuals/cm² with a lake average of 136 individuals/cm². Correspondingly, the settled volume ranged from 7.8 to 13.3 mm³/cm² with a lake average of 10.9 mm³/cm².

Lake Wood — Only six species were found in Lake Wood with *C. bicuspidatus thomasi* (55.6%) and *D. ashlandi* (41.5%) dominant (Table 4). As in Lake Skaha and Osoyoos, a high percentage of the population consisted of adults. Only three species of cladocerans were encountered in this lake, *D. leuchtenbergianum*, *D. longiremis*, and *L. kindtii*, together constituting no more than 2.2% of the total number of 139 individuals/cm². A rather high settled plankton volume, 31.3 mm³/cm², in relation to the numbers of individuals, was mainly due to a high share of adults in the population and a high amount of phytoplankton.

TOTAL PHOSPHORUS LOAD AS A MEASURE OF EUTROPHICATION OF THE LAKES OF THE OKANAGAN VALLEY

The classical terms oligo-, meso-, and eu-trophy in the sense of Thienemann (1928) and Naumann (1931) are quite useful for describing the general trophic character of lakes, but they are inadequate for comparing them quantitatively. The concept of nutrient loading rate, developed by Vollenweider

(1968, 1969), was applied in this paper as one of the simple measures of eutrophication related to both autotrophic and allotrophic organic production in the lake. The total phosphorus load to lakes Okanagan, Skaha, and Osoyoos was calculated in two ways: 1) based on the data of Alcock and Clarke (1968) and 2) based on Vollenweider's (1968) estimates of phosphorus "export" from the soils and contribution by human population.

Using the former authors' data, 10 creeks (Otter, Vernon, Whitemens, Brant's, Mill, Mission, Sawmill, Powers, Trepanier, and Trout), with an annual flow of $255.66 \cdot 10^6$ m^3 and an average concentration of 0.17 g/m^3 total P, contributed 42,800-kg total P to Okanagan Lake in 1968. The total annual surface inflow (runoff) to Okanagan Lake, calculated as the sum of the recorded discharge and evaporation (Anon. 1967–70) from the lake surface minus precipitation on the lake surface, equals $(450.22 + 271.2 - 103.3) \cdot 10^6$ m^3 $= 618.1 \cdot 10^6$ m^3. Assuming that the remaining sources, unrecorded by Alcock and Clarke, contributed phosphorus in the same concentration as did the ten creeks, the loading from all creeks should amount to $\frac{618.1}{255.6} \cdot 42{,}800$ kg/year total P, 103,480-kg P. In addition, contribution of the sewage treatment plant in Kelowna was 25,950-kg P and that of the West Bank sewage treatment plant was 180-kg P for a total of 129,610-kg/yr total P, or 0.38-g/m^2·year total P.

TABLE 3. Distribution of species in the upper 5-m layer of inshore and offshore waters of Lake Okanagan. August 25–26, 1971. (individuals/liter)

Transect	Station	*Epischura nevadensis*	*Diaptomus ashlandi* copepodids	*Diaptomus ashlandi* nauplii	*Cyclops bicuspidatus thomasi* copepodids	*Cyclops bicuspidatus thomasi* nauplii	*Daphnia thorata*	*Bosmina longirostris*	*Diaphanosoma leuchtenbergianum*	Total
I	Inshore									
	East	0.98	5.8	1.2	1.0	0.32	0.48	0.12	0.10	10.2
	Offshore	7.0	4.4	6.6	5.2	0.30	2.4	0.46	0.62	27.2
II	In West	9.6	2.6	2.8	1.6	0.48	0.94	0.40	0.08	9.6
	In East	1.0	3.8	3.4	1.4	0.54	0.86	0.10	0.12	11.2
	Off	0.46	19.0	1.6	5.2	1.4	3.8	0.46	0.46	32.4
IV	In West	0.68	12.6	0.8	5.4	0.38	2.4	0.54	0.20	23.6
	In East	0.86	4.2	3.0	3.0	0.38	1.44	0.10	0.34	13.6
	Off	0.20	27.4	0.4	12.0	0.0	0.62	1.24	0.42	42.6
V	In East	1.04	3.2	4.0	1.64	0.2	0.54	0.28	0.12	11.6
	Off	1.04	9.6	1.0	7.0	0.6	3.2	0.0	0.2	23.2
VI	In West	0.64	3.8	1.0	3.6	0.14	2.24	0.36	0.24	14.4
	In East	1.10	2.8	5.4	3.8	0.26	1.08	0.52	0.16	15.6
	Off	1.32	2.0	7.2	4.6	0.36	1.68	0.26	0.08	18.0
VII	In West	0.98	7.8	1.8	3.4	0.38	1.04	1.2	0.48	16.6
	In East	1.26	0.8	9.6	2.8	0.50	0.56	0.28	0.08	16.4
	Off	1.68	11.2	2.0	6.0	0.70	3.0	0.44	0.36	25.4
X	In West	1.36	1.8	1.4	0.68	0.24	0.32	0.68	1.0	7.6
	Off	0.62	16.2	1.0	1.34	0.30	0.62	0.20	2.4	23.4
Mean	Inshore	0.95	4.5	3.0	2.6	0.33	1.1	0.41	0.26	13.6
	Offshore	1.75	12.8	2.9	5.8	0.52	2.1	0.44	0.64	27.6
$\frac{\text{Offshore}}{\text{Inshore}}$	ratio	1.8	2.8	0.97	2.2	1.6	1.9	1.1	2.5	2.0

TABLE 4. Species composition of crustacean plankton (individuals per cm²) in lakes Skaha and Osoyoos, on September 11, 1969 and August 24, 1971 and in lakes Wood and Kalamalka on August 26, 1971. Figures for August 1971 in italics.

	Station	Depth (m)	*Epischura nevadensis* Lilljeborg	*Diaptomus ashlandi* Marsh			*Cyclops bicuspidatus thomasi* Forbes			*Cyclops vernalis* Fischer	*Daphnia thorata* Forbes	*Daphnia longiremis* Sars	*Daphnia schoedleri* Sars	*Daphnia pulex* Leydig	*Bosmina longirostris* (O. F. Müller)	*Bosmina coregoni longispina* Leydig	*Diaphanosoma leuchtenbergianum* Fischer	*Leptodora kindtii* (Focke)	Total
				adult	copepodid	nauplius	adult	copepodid	nauplius										
									Skaha										
	S	39	2.6	18.5	54.8	40.8	–	30.0	53.1	–	1.1	2.9	0.1	–	0.1	–	2.7	<0.1	206.7
		50	*3.7*	*7.8*	*18.6*	*46.5*	*3.1*	*93.0*	*114.7*	*1.6*	*0.6*	*1.9*	–	*1.5*	–	*<0.1*	*4.7*	*0.1*	*297.7*
	C	52	2.2	25.4	58.5	43.1	2.3	40.0	73.9	–	0.2	4.5	0.2	<0.1	0.1	–	2.3	<0.1	252.7
		50	*2.3*	*11.6*	*26.3*	*37.9*	*1.6*	*46.5*	*105.3*	–	*1.2*	*4.2*	–	*2.2*	–	*0.2*	*5.4*	*0.1*	*244.7*
	N	44	2.6	27.7	62.5	43.9	30.8	29.2	54.7	–	0.5	1.4	0.1	–	0.1	–	1.3	–	254.8
		50	*5.1*	*11.6*	*29.4*	*14.7*	*3.1*	*20.1*	*65.8*	–	*0.9*	*0.5*	–	*1.1*	*0.1*	–	*5.4*	*0.1*	*158.1*
			2.5	23.9	58.6	42.6	11.0	33.1	60.6	–	0.6	3.0	0.1	0.1	<0.1	–	2.1	<0.1	238.1
Lake avg			*3.7*	*10.3*	*24.8*	*33.0*	*2.6*	*53.2*	*95.3*	*0.5*	*0.9*	*2.2*	–	*1.6*	–	*0.1*	*5.1*	*0.1*	*233.5*
ind./cm²			1.0	10.0	24.6	17.9	4.6	13.9	25.4	–	0.3	1.2	0.1	<0.1	<0.1	–	0.9	<0.1	100.0
%			*1.6*	*4.4*	*10.6*	*14.1*	*1.1*	*22.8*	*40.8*	*0.2*	*0.4*	*0.9*	–	*0.7*	–	*<0.1*	*2.2*	*<0.1*	*100.0*
									Osoyoos										
	C	24	0.3	8.7	30.8	29.2	5.1	20.0	40.6	<0.1	0.5	–	–	<0.1	0.6	–	3.7	<0.1	139.5
		26	*1.4*	*3.1*	*2.2*	*14.9*	*1.2*	*9.6*	*22.9*	*1.2*	*<0.1*	–	–	*<0.1*	*<0.1*	–	*1.2*	*<0.1*	*57.9*
	N	29	0.2	20.8	63.9	36.9	8.5	10.8	30.8	–	0.8	0.5	0.1	–	<0.1	–	10.0	0.1	183.4
		50	*2.5*	*5.7*	*14.0*	*14.6*	*1.6*	*9.4*	*35.9*	*0.3*	*0.4*	*2.4*	–	*0.5*	–	–	*6.8*	*<0.1*	*93.8*
			0.2	14.8	47.4	33.0	6.8	15.4	35.7	<0.1	0.7	0.3	<0.1	–	0.3	–	6.8	0.1	161.4
Lake avg			*2.0*	*4.4*	*8.1*	*14.8*	*1.4*	*9.5*	*29.4*	*0.8*	*0.2*	*1.2*	–	*0.3*	*<0.1*	–	*4.0*	*<0.1*	*75.9*
ind./cm²			0.1	9.1	29.3	20.5	4.2	9.5	22.1	0.1	0.4	0.2	<0.1	–	0.2	–	4.2	<0.1	100.0
%			*2.6*	*5.8*	*10.6*	*19.4*	*1.8*	*12.5*	*38.6*	*1.1*	*0.3*	*1.6*	–	*0.4*	*<0.1*	–	*5.3*	*<0.1*	*100.0*
									Kalamalka										
	S	31	*3.8*	–	*35.9*	*0.5*	–	*35.4*	*14.6*	–	*2.6*	*6.2*	–	–	*<0.1*	*0.1*	*1.6*	–	*100.7*
	SC	50	*2.8*	–	*51.9*	*3.1*	*0.1*	*64.3*	*20.1*	–	*2.3*	*7.0*	–	–	*0.4*	*0.1*	–	–	*152.0*
	NC	40	*3.9*	–	*55.8*	*1.6*	*0.8*	*53.4*	*39.5*	–	–	*13.2*	–	–	*0.4*	*0.6*	–	*<0.1*	*169.1*
	N	50	*5.3*	–	*27.0*	*0.5*	–	*48.4*	*22.9*	–	*3.1*	*5.2*	–	–	*3.1*	*0.5*	*<0.1*	–	*116.0*
	NE	50	*4.8*	–	*34.8*	*0.8*	–	*44.9*	*37.9*	–	*2.3*	*11.6*	–	–	*2.3*	*1.6*	–	–	*141.0*
Lake avg																			
ind./cm²			*4.1*	–	*41.1*	*1.3*	*0.2*	*49.3*	*27.0*	–	*2.1*	*8.6*	–	–	*1.2*	*0.6*	*0.3*	*<0.1*	*135.8*
%			*3.0*	–	*30.3*	*1.0*	*0.1*	*36.3*	*19.9*	–	*1.5*	*6.3*	–	–	*0.9*	*0.4*	*0.2*	*<0.1*	*100.0*
									Wood										
	S	27	*1.1*	*6.2*	*47.8*	*8.8*	*6.2*	*12.5*	*39.5*	–	–	*<0.1*	–	–	–	–	*0.5*	*<0.1*	*122.8*
	N	26	*0.9*	*7.0*	*39.5*	*6.2*	*13.2*	*30.2*	*52.7*	–	–	*0.8*	–	–	–	–	*4.7*	*<0.1*	*155.2*
Lake avg																			
ind./cm²			*1.0*	*6.6*	*43.7*	*7.5*	*9.7*	*21.4*	*46.1*	–	–	*0.4*	–	–	–	–	*2.6*	*<0.1*	*139.0*
%			*0.7*	*4.7*	*31.4*	*5.4*	*7.0*	*15.4*	*33.2*	–	–	*0.3*	–	–	–	–	*1.9*	*<0.1*	*100.0*

To determine what portion of this load reached Skaha Lake, it was necessary to estimate the retention of phosphorus within Okanagan Lake. Based on Vollenweider (1968) data, and taking into account a very slow water renewal (volume: discharge = 59 years), a high retention coefficient of 0.95 was assumed for Okanagan Lake, and a lower one, 0.65, for Skaha Lake with a much shorter renewal time of 1.1 years. The total phosphorus load to Lake Skaha can then be calculated as follows:

Okanagan River carrying to Lake Skaha 5% of the annual Lake Okanagan load, $0.05 \cdot 129{,}610$ kg =	6480-kg P
Penticton sewage treatment plant contribution =	15,200-kg P
The annual surface inflow (runoff) to Lake Skaha from the drainage basin below Penticton, calculated as the sum of Skaha discharge and evaporation from the lake surface minus precipitation on the lake surface minus the Okanagan River inflow equals $(473.66 + 16.367 - 5.984 - 450.22) \cdot 10^6$ m^3 = $33.832 \cdot 10^6$ m^3. Assuming that the concentration of phosphorus in all the surface inflow is equal to the mean concentration in 10 Okanagan Lake tributaries, the loading will amount to $33.823 \cdot 10^6$ m$^3 \cdot 0.17$ g/m^3 total P =	5750-kg P
Total	27,430-kg P
or 1.4 g/m^2·year total P.	

In a similar way, the phosphorus load to Lake Osoyoos can be calculated as follows:

Okanagan River carrying to Lake Osoyoos 35% of the annual Lake Skaha load, $0.35 \cdot 27{,}430$ kg =	9600-kg P
The Oliver sewage treatment plant contribution =	2630-kg P
Contribution from the drainage below Skaha Lake, calculated as the sum of the Osoyoos Lake discharge and evaporation from the lake surface minus precipitation on the lake surface minus the Lake Skaha discharge, multiplied by the average concentration of total phosphorus, equals $(510.66 + 8.046 - 3.067 - 473.66) \cdot 10^6m^3 \cdot 0.17$ g/m^3 total P =	7136-kg P
Total	19,366-kg P
or 2.0 g/m^2·year total P.	

The other method of phosphorus loading calculation is based on Vollenweider's (1968) estimate of phosphorus "export" from the soil and the phosphorus contribution by human population. According to this author, the total phosphorus export from polytrophic soils is greater than 0.05 g/m^2·year total P, from mesotrophic soils between 0.02 and 0.05, and from oligotrophic soils less than 0.02 g/m^2·year total P. For lakes Okanagan, Skaha, Osoyoos, and Kalamalka an export value as low as 0.005 g/m^2·year total P (i.e. the lowest quarter in the oligotrophic range) was applied, taking into account that more than 90% of the drainage basin consists of oligotrophic, rough mountainous land (Kelley and Spilsbury 1949), and that the narrow strip of arrable land around the lakes receives very low precipitation, on the average 320 mm per year for Vernon, Kelowna, and Penticton, and 270 mm per year for Oliver and Osoyoos. The value 0.010 g/m^2 was applied for the Wood Lake drainage taking into account the very intensive irrigation in this area. According to Vollenweider (1968), the contribution of total phosphorus by a human population inhabiting a representative basin area with a density of 150 inhabitants/km^2 amounts to 0.17–0.25 g/m^2·year total P. Taking into account the high level of intensification of horticulture in the Okanagan Valley, the upper value of 0.25 g/m^2·year was selected, corresponding to a loading of 1.7 kg/capita·year total P. It was felt that this figure should even be increased to 2.0 kg/capita for Wood Lake since its basin, with 35% of its area under irrigation, supported a very intensive horticultural practice. For calculation of loads in the past, 0.7 kg/capita in 1850 and 1.0–1.2 kg/capita·year total P in 1921–1935 was applied, taking into account that no detergents were in use at that time. Today, they contribute about 50% of the phosphorus from human sources (Anon. 1969).

The formula for total phosphorus load (L_p in grams per square meter of lake surface·year total P) may be presented in the following form:[1]

$$L_p = \frac{E_s \cdot A_d}{A_o} + \frac{E_c \cdot C}{A_o} + \frac{(1-R_a) L_{pa} \cdot A_{o(a)}}{A_o}$$

where:

- E_s = "Export" of phosphorus from the soil in grams per square meter of the land drainage·year total P;
- A_d = Area of the land drainage in square meters;
- A_o = Area of the lake in square meters;
- E_c = Per capita discharge of phosphorus reaching the lake in grams per capita·total P;
- C = Basin population;
- R_a = Total P retention coefficient in the next lake upstream to the lake considered;

[1]The phosphorus supplied by precipitation was not included here as the precipitation is very low in this area. It can contribute about 0.02 g/m^2 of lake area·year total P (Vollenweider 1968). It can be a significant part of the total load in lakes within poor soil areas as demonstrated by Schindler and Nighswander (1970) and Armstrong and Schindler (1971).

L_{pa} = Total P load in the next lake upstream to the lake considered in grams per square meter ·year total P;

$A_{o(a)}$ = Area of the next lake upstream to the lake considered.

The basic data used, as well as the method of calculation, are presented in Table 5. An interesting comparison is provided by the results of the two calculations of phosphorus load based on the two independent methods:

Lake:	Okanagan	Skaha	Osoyoos
	g/m²·year total P		
Analyses of P concentrations and flow rates (data of Alcock and Clarke 1968)	0.38	1.4	2.0
Estimates of P export from soil and contribution by human population, based on Vollenweider's criteria (1968)	0.39	2.2	2.7

There were no significant differences between both estimates of Okanagan Lake loading. The values for Lakes Skaha and Osoyoos estimated according to Vollenweider criteria were only about 60 and 30% higher, respectively, than those calculated from Alcock and Clarke's data. These differences can be regarded as small if taking into account the many assumptions that had to be made for the calculation. They also indicate that the loading rates calculated for Lake Kalamalka (0.32-g/m²·year total P) and Wood (0.50-g/m²·year total P) using Vollenweider's criteria compare well with the other lake loadings. Thus, the advantage of this method is that some estimates of loading rates in the past or predictions for the future could be made.

Hypolimnetic Areal Oxygen Deficit as a Measure of the Eutrophication of Lakes of the Okanagan Valley

The rate of depletion of oxygen in the hypolimnion during the period between vernal circulation and the height of summer stratification can, according to Hutchinson (1957), provide a good indication of the biological productivity of holomictic lakes ranging 20–75 m in depth. This relation breaks down for different reasons in both shallower and deeper lakes. Deficits could be calculated only for Lakes Skaha, Osoyoos, and Wood since they alone fell within this depth range. In this calculation, it was assumed that the hypolimnetic waters were saturated with oxygen during the spring overturn. The hypolimnetic areal deficits were similar in all three lakes and amounted to 0.076- and 0.077-mg/cm²·day O_2 in Lake Skaha, 0.077- and 0.086-mg/cm²·day O_2 in Lake Osoyoos, and 0.080-mg/cm²·day O_2 in Lake Wood. The details of calculations are presented in Table 6.

Discussion

On the basis of two series (1969, 1971) of late summer measurements of such parameters as temperature, water transparency, oxygen, and some macroelements, it appears that in Okanagan Lake at least four basins that demonstrate various conditions can be distinguished: (1) A southern basin (Penticton, Summerland) represented by transect I and II, characterized by the deepest epilimnion, the lowest content of dissolved solids, and a relatively lower transparency; (2) The Peachland–Kelowna basin (transects IV and V) with an epilimnion shallower than in the southern basin, a significantly different position of the thermocline as compared with that north of the bridge (transect VI), and intermediate Secchi disc transparency; (3) The deepest part of the lake north of Kelowna (transects VI–VIII), with a shallower epilimnion, the greatest transparency, and the highest total dissolved solids; (4) The northern end of the lake (transect X), the shallowest basin with a relatively warmer hypolimnion, highest calcium content, highest conductivity, lowest transparency, and lowest oxygen content in the hypolimnion. Transect III assumes an intermediate position between the first and the second basins, while transect IX appears to be an intermediate zone between the third and fourth basins. This scheme of basin distinction should be taken into consideration when planning any general limnological study on this lake.

Data of Rawson (1939), describing the situation in Lake Okanagan during the summer of 1935, were compared to the present data of 1969 and 1971 in Table 7. No significant differences in Secchi disc visibility were found among these three sets of data. There appears to have been no apparent decrease in the oxygen concentration of the hypolimnetic waters since 1935. Although a slightly higher saturation value of 94% was found in 1969 and 1971 as compared with 88% in 1935, this variation can be interpreted as an annual fluctuation rather than a real long-term trend. A single chemical analysis of a water sample taken in the central part of the lake in April 1936 showed 145-mg/liter total dissolved solids (TDS) and 28.7-mg/liter Ca. In 1969, the value of 164-mg/liter TDS was 19 mg/liter greater than the TDS 33 years earlier in 1936. Also, the calcium

TABLE 5. Some limnological characteristics and parameters used for calculation of total phosphorus load to the lakes of the Okanagan Valley according to Vollenweider's criteria (1968).[a]

	Symbols	Year	Lakes				
			Okanagan	Skaha	Osoyoos (Northern basin)	Kalamalka	Wood
Area of the lake in $10^6 m^2$	A_o		344.4	20.137	9.899	25.9	9.3
Area of the land drainage in 10^6 m^2	A_d		6060.6	828.8	1269	192	55
Ratio of the land drainage to lake area	$\frac{A_d}{A_o}$		17	41	128	7.4	5.9
Max. depth (m)	Zm		242	55.8	63.4	141.0	34.0
Mean depth (m)	$\bar{Z}$		75.3	26.5	20.7	58.0	21.0
Vol. km^3	V		26.000	0.53192	0.204743	1.500	0.196
Discharge km^3·year	D		0.450221	0.473657	0.510661	0.013878	0.00181
Relative annual discharge	$\frac{D}{V}$		0.017	0.89	2.5	0.009	0.0092
Basin population	C	1850	2,000	500	200	200	100
		1921	17,000	5000	500	1000	500
		1935	21,000	8000	1000	1500	800
		1969	60,000	20,000	3000	4000	2000
		1990	110,000	36,000	5500	7000	3600
Export of phosphorus from the soil in g/m^2 of land·year total P	E_s		0.005	0.005	0.005	0.005	0.01
Per capita discharge of phosphorus reaching the lake in g/year total P	E_c	1850	700	700	700	700	700
		1921–35	1000	1000	1000	1000	1200
		1969–90	1700	1700	1700	1700	2000
Retention of phosphorus in the lake in relation to the phosphorus load	R		0.95	0.65	–	0.90	0.90
Calculations of load (in g/m^2 of lake·year total P)							
Phosphorus load from soil $E_s \cdot A_d/A_o$	l_s		0.09	0.20	0.64	0.04	0.06
Population dependent phosphorus load $\frac{E_c \cdot C}{A_o}$	l_c	1850	0.009	0.017	0.014	0.005	0.01
		1921	0.05	0.25	0.05	0.04	0.07
		1935	0.06	0.40	0.10	0.06	0.10
		1969	0.30	1.68	0.51	0.26	0.43
		1990a	0.54	3.04	0.94	0.46	0.77
		1990b	0.10	0.61	0.19	0.09	0.15
Phosphorus load from the lake above $(1-R) \cdot L_{p4} \cdot \frac{A_{o(a)}}{A_o}$	l_a	1850	0.0	0.08	0.23	0.003	0.01
		1921	0.0	0.12	0.42	0.005	0.01
		1935	0.0	0.13	0.50	0.006	0.01
		1969	0.0	0.33	1.56	0.02	0.01
		1990a	0.0	0.54	2.66	0.03	0.01
		1990b	0.0	0.17	0.67	0.01	0.01
Total phosphorus load from all sources $l_s + l_c + l_a$	L_p	1850	0.09	0.3	0.9	0.05	0.08
		1921	0.14	0.6	1.1	0.09	0.14
		1935	0.15	0.7	1.2	0.11	0.17
		1969	0.39	2.2	2.7	0.32	0.50
		1990a	0.63	3.7	4.2	0.53	0.84
		1990b	0.19	0.9	1.5	0.14	0.22

[a]Notes: Morphometric data of the lakes taken from bathymetric maps prepared by the Fish and Wildlife Branch, Dep. of Recreation and Conservation in 1966 (J. A. Balkwill).
Area of drainage basin according to Coulthard and Stein (1967). Discharge from Alcock and Clarke (1968).
Populations estimates 1850–1990 according to Anon. (1971).
Phosphorus retention (R) estimates based on Vollenweider (1968).
Predicted P load estimates in 1990 based on assumptions: a) no phosphorus removal; b) 80% phosphorus removed in controllable sources.

TABLE 6. Parameters used for calculation of hypolimnetic areal oxygen deficit of lakes Skaha, Osoyoos, and Wood. (Figures for 1971 in italics).

	Symbol	Lake Skaha	Lake Osoyoos (northern part)	Lake Wood
The area of the 20 m izobath accepted as the upper limit of the hypolimnion in $cm^2 \cdot 10^{10}$	A_{20}	10.115	4.855	4.95
The volume of the lake below the 20 m izobath in liters$\cdot 10^{10}$	V_{20}	22.346	7.1514	4.15
The weighted average of the hypolimnetic temperature in C September 11, 1969, August 24–25, 1971.	$\bar{T}<20$	7.0 *7.4*	7.9 *9.4*	*6.0*
The weighted average concentration of oxygen in hypolimnion in mg/liter O_2, September 11, 1969, August 24–25, 1971	O_2S	7.3 *7.4*	3.9 *4.8*	
The assumed hypolimnetic oxygen concentration in mg/liter O_2 on May 1, 1969, May 1, 1971.	O_2M	11.8 *11.6*	11.5 *11.1*	*12.2*
Hypolimnetic areal oxygen deficit in mg/cm^2·day O_2 during the period May 1–September 11, 1969, May 1–August 24–25, 1971.	$\frac{(\bar{O}_2M-\bar{O}_2S)\cdot V_{20}}{A_{20}\cdot 130\ (120)\ \text{days}}$	0.076 *0.077*	0.086 *0.077*	*0.80*

TABLE 7. A comparison of several limnological characteristics of lakes of Okanagan Valley, and lakes Ontario, Mendota, and Washington. Lake means, except where indicated. 1935 and 1936 data taken from Rawson (1939).

Lake	Date	Secchi disc visibility (*m*)	Oxygen in hypolimnion, percentage of saturation	Hypolimnetic oxygen areal deficit mg/cm^2·day O_2 May–Aug. (Sept.)	Total dissolved solids mg/liter	Calcium mg/liter Ca	Phosphorus load g/m^2·year total p	Zooplankton crustaceans ind./cm^2	Zooplankton crustaceans mm^3/cm^2
Okanagan	Aug. 1935	(8.0–10.0)[a]	88[a]		145[b]	28.7[b]	0.15		2.8
	Sept. 9–10, '69	8.5(9.0[a])	88(94[a])		164	31.9	0.39	188	13.3
	Aug. 26–27, '71	9.4(10.9[a])	89(94[a])			35.1		101	7.8
Skaha	Sept. 11, '69	2.7	60	0.076	164.3	31.3	2.2	238	23.2
	Aug. 24, '71	5.3	63	0.077	195.7	33.8		236	24.1
Osoyoos	Sept. 11, '69	4.1	20	0.086	168.5	31.5	2.7	161	25.9
	Aug. 24, '71	4.0	22	0.077	169.0	33.3		76	10.9
Kalamalka	Aug. 14, '35	(6.0–7.0)	87				0.11		4.5
	Aug. 25, '71	5.7	95		252	37.3	0.32	136	10.9
Wood	Aug. 13, '35	(2.0–2.5)	21				0.17		15.4
	Aug. 25, '71	3.9	5	0.080	211.5	21.8	0.50	139	31.1
Ontario[c]	Sept. '67	4.1	95		185	42.9	0.65	320	44.9
Mendota[d]			<0.5	0.109			>0.55		
Washington[e]	1957	2.0	42	0.086			1.06	ca.300	

[a]Mean value of Peachland–Kelowna area.
[b]April 1936, sample taken between Peachland and Kelowna.
[c]Data from Patalas (1969) and Anon. (1969).
[d]Date from Hutchinson (1957) and Edmondson (1969).
[e]Data from Edmondson (1966, 1969).

content was higher both in 1969 (31.9-mg/liter Ca) and 1971 (35.1-mg/liter Ca). It is difficult, however, to say whether the 3.2–6.4-mg/liter Ca increase is a significant one or whether it can still be interpreted as a season to season fluctuation.

The lists of crustacean species found in the summer months of 1935 in Lakes Okanagan and Kalamalka (Rawson 1939) were compared with those from 1951, 1969, and 1971 (Table 8).

D. ashlandi and *C. bicuspidatus thomasi* still remained the dominant forms in the latter years. *Diaptomus* sp. in 1935 in Lake Kalamalka probably refers to *D. ashlandi* Marsh, and *C. bicuspidatus* Claus from 1935 was certainly *C. bicuspidatus thomasi* Forbes. *D. thorata* Forbes and *D. longiremis* Sars, identified in this paper according to Brooks (1957), may correspond to the specific name *D. longispina* (O. F. Müller) used by Rawson (1939) in accordance with contemporary taxonomy. *B. longispina* Leydig is certainly a synonym of *B. coregoni longispina* Leydig or *Eubosmina longispina* (Leydig) used recently by Deevey and Deevey (1971). *Diaphanosoma leuchtenbergianum* Fischer was considered by some authors as a limnetic variety of *D. brachyurum* Lievin (Brooks 1957), hence both recent and 1935 identifications probably refer to the same animal. No conclusion can be drawn on the presence or absence of a few species found as single specimens in 1969 and 1971 (*C. vernalis*, *D. pulex*, *S. crystallina*, *H. gibberum*). *B. longirostris* could be easily overlooked in the Lake Okanagan sample from 1935, as it was also very rare in 1951 samples. Taking all the nomenclatoric and other problems into account, the conclusion should be drawn that no substantial changes have occurred since 1935 in the species composition of lakes Okanagan and Kalamalka. The only significant difference between 1935 and 1969–71 samples seems to involve zooplanktonic abundance. The average volume of settled plankton for 11 total vertical hauls taken by Rawson between July 4 and August 26, 1935, in the southern, central, and northern parts of Okanagan Lake was 1.4 cm^3 or 2.8 mm^3/cm^2. Samples taken on September 9 and 10, 1969, and August 26–27, 1971, using a Wisconsin net comparable to that used in 1935, revealed an average of 13.3 and 7.8 mm^3/cm^2,

TABLE 8. List of species found in net plankton of lakes Okanagan and Kalamalka in the period from 1935 to 1971. (1935 data taken from Rawson 1939), identifications by Dr G. C. Carl; 1951 data, identifications by present authors from samples kindly provided by Dr T. G. Northcote.)

	Okanagan				Kalamalka		
Species	July–Aug. 1935	July 25, 1951	Sept. 9–16, 1969	Aug. 24–26, 1971	Aug. 14, 1935	July 31, 1951	Aug. 25, 1971
Epischura nevadensis Lilljeborg	×[a]	×	×	×	×	×	×
Diaptomus ashlandi Marsh	××	××	××	××	(××)	××	××
Diaptomus sp.					××		
Cyclops bicuspidatus thomasi Forbes	(××)	××	××	××	(××)	××	××
Cyclops bicuspidatus Claus	××				××		
Cyclops vernalis Fischer				·			
Daphnia longispina (O. F. Müller)	×				×		
Daphnia thorata Forbes	(×)	×	×	×	(×)	×	×
Daphnia longiremis Sars	(×)	×	×	×	(×)	×	×
Daphnia pulex Leydig				·		·	
Daphnia schoedleri Sars (× pulex)				·			
Scapholeberis mucronata (O. F. Müller)	·				·		
Bosmina longirostris (O. F. Müller)		·	×	×	×	×	×
Bosmina coregoni longispina Leydig	×[b]	×	×	×		×	×
Diaphanosoma brachyurum Lievin	×						
Diaphanosoma leuchtenbergianum Fischer	(×)	×	×	×		·	×
Sida crystallina (O. F. Müller)	·			·			
Leptodora kindtii (Focke)	·	·	·	·		·	·
Holopedium gibberum Zaddach	·						

[a] ××, abundant species above 10% of the total number of crustaceans; ×, common but not abundant 0.1–10.0%; ·, rare — less than 0.1%; The marks in parentheses denote the probable names according to presently used taxonomy.

[b] Listed as *Bosmina longispina* Leydig.

respectively, i.e. 4.8 and 2.8 times more than in 1935 (Table 7). Even assuming that sampling in September 1969 hit the late summer maximum of zooplankton, the almost 3–5 times higher values in 1969 and 1971 indicate an apparent increase in the abundance of zooplankton since Rawson's 1935 studies. This increase is paralleled by an approximate eight fold increase in the total abundance of bottom organisms in 1969 (Saether 1970) as compared with the Rawson data from 1935. Although much higher zooplankton amounts were observed in 1969 and 1971, there were no accompanying changes in Secchi disc visibility and in hypolimnetic oxygen deficit. A probable source for the increased abundance in offshore waters is the littoral zone, which is affected by increasing eutrophication sooner than offshore waters. This explanation is to a certain degree in agreement with Saether's findings (1970), i.e. that between 1935 and 1969 the highest increase in the numbers of bottom organisms occurred in shallower, nearshore stations while the deep, profundal zone remained unchanged both in qualitative and in quantitative aspects. Also, preliminary results of periphyton studies (Stockner 1970) indicate a much higher local algal growth in the littoral zone of Okanagan Lake than could be expected from the transparency of offshore waters. This accumulation of plants and animals in the littoral zone due to eutrophication phenomena rather concerns the sessile components of the aquatic community. Most of the planktonic crustaceans, except *B. longirostris* and the nauplial stages of *Diaptomus*, were found less abundant in inshore waters (Table 3), likely a resultant of horizontal currents, vertical migrations (Burckhardt 1910), and, also, shore avoidance reactions as demonstrated by Siebeck (1964).

The numbers of zooplanktonic crustaceans in the lakes of the Okanagan Valley are similar to those found during comparable times in several Great Lakes (Patalas 1972):

Lake	Individuals/cm²
Superior	43
Huron	167
Ontario	306
Erie	400
Okanagan	101–188
Kalamalka	136
Wood	139
Osoyoos	76–161
Skaha	236–238

Lakes of the Okanagan Valley are apparently richer in plankton than Lake Superior but poorer than lakes Erie and Ontario. The figures for lakes Skaha, Osoyoos, and Wood can be interpreted as being quite high if one bears in mind that the very high flushing rate of the first two lakes does not favour the accumulation of plankters produced in the lake. In addition, the very low oxygen content in the hypolimnia of lakes Osoyoos and Wood restricts the inhabitable layer to approximate the upper 20 m as compared to 50 m in the remaining lakes.

The phosphorus loads to the lakes of the Okanagan Valley are plotted on Fig. 13 (taken from Anon. 1969, originally constructed by Vollenweider 1968) to compare their state of trophy with that of some other American lakes. The essence of this conclusive graph is that the same P load per unit of lake area affects to a much greater degree a shallower lake than a deeper one with a larger volume of water. Lakes plotted on the graph below the lower line are oligotrophic, those above the upper line are eutrophic. Mesotrophic lakes approaching the eutrophic stage are situated between the two lines. The vertical distance above the upper line can be considered as a measure of the eutrophication.

The estimates of the present phosphorus load to Lake Okanagan, 0.39- and to Lake Kalamalka, 0.32-g/m²·year total P, indicate that these lakes are still in the oligotrophic range, but close to the mesotrophic level. Since Lake Wood is much shallower than the previous two, the relatively similar load of 0.50-g/m²·year total P puts it in the moderately eutrophic range. Lakes Skaha and Osoyoos with a loading of 2.2- and 2.7-g/m²·year total P, respectively, show a marked degree of eutrophy,

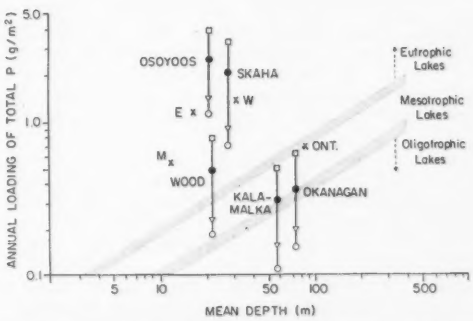

FIG. 13. Annual total phosphorus load to lakes Okanagan, Skaha, Osoyoos, Kalamalka, and Wood as compared with a number of lakes in North America calculated after Vollenweider (1968) and Anon. (1969). Open circles denote values estimated for 1935; black dots — for 1969. Predicted load estimates for the year 1990 assuming no phosphorus removal are indicated by quadrangles and assuming 80% phosphorus removal from controllable sources — by triangles. Crosses denote loadings to lakes Erie (E), Ontario (ONT), Mendota (M), and Washington (W) before sewage diversion in 1957.

possibly slightly overestimated when one takes into account that, due to a high rate of water renewal (Table 5), a significant part of the incoming nutrients are removed from the lake with the outflowing water within the same season. Even after this correction, the loadings in these two lakes will probably be higher than e.g. that in Lake Washington before sewage diversion (1.06-g/m^2·year total P) and Lake Erie (1.06-g/m^2·year total P). These conclusions can be further supported by the estimates of the hypolimnetic areal oxygen deficit (Table 6). According to Hutchinson (1957), the hypolimnetic areal deficits are:

In oligotrophic lakes	0.004–0.033-mg/cm^2·day O_2
In mesotrophic lakes	0.033–0.050-mg/cm^2·day O_2
In eutrophic lakes	0.050–0.140-mg/cm^2·day O_2

The deficits for Lakes Skaha, Osoyoos, and Wood were within a relatively narrow range, 0.076–0.086-mg/cm^2 O_2, all well above the lower limit of the eutrophic range, or about its middle portion. The values are comparable to some well known eutrophic lakes like Lake Mendota, Wisconsin (0.109-mg/cm^2·day O_2), or Furesø in Denmark (0.080-mg/cm^2·day O_2). The value 0.086-mg/cm^2·day O_2 found in Lake Osoyoos corresponds precisely to the value found by Edmondson (1966) in Lake Washington before sewage diversion.

The apparent agreement between the different independent indices of eutrophication of the Okanagan Valley lakes increases the probability that these estimates are a good approximation of the true situation.

Another important conclusion can be drawn from the analysis of the origin of phosphorus supplied to the lakes (Table 5). In 1969, 77% of the total phosphorus load to Okanagan Lake was associated with the human population (industrial pollution, municipal sewage and agriculture); the corresponding values for Skaha Lake were 88%, for Osoyoos Lake 72%, for Kalamalka Lake 81%, and for Wood Lake 86%. Such a high contribution of phosphorus from population dependent sources indicates that a program of phosphorus removal from the controllable sources is justified and has a good chance in reversing the present trend of eutrophication.

Based on past changes in the population density in the Okanagan Valley and expected population growth in the future (Okanagan–Shushwap Region, 1971), the phosphorus loading rates were calculated for the years 1850, 1921, 1935, 1969, and 1990. Assumptions were made that the phosphorus load from the soil (l_s) and the phosphorus retention

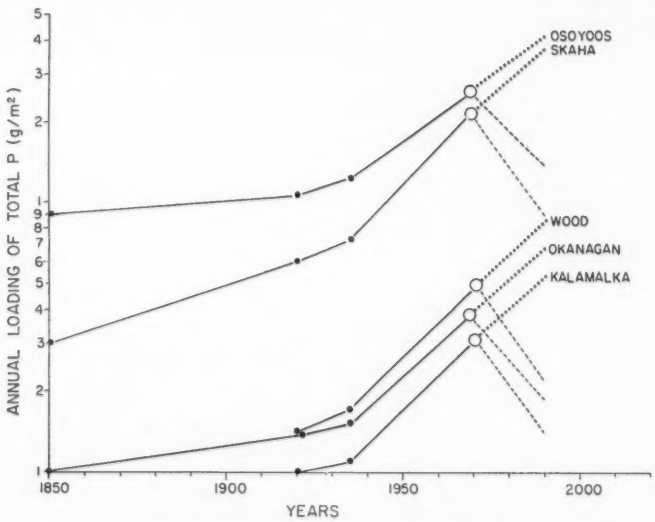

FIG. 14. Estimated changes in total phosphorus load to the lakes of the Okanagan Valley between 1850 and 1990. Open circles denote the load in 1969 or 1971; dotted lines denote predicted load assuming no phosphorus removal; the broken lines denote predicted load assuming 80% phosphorus removal from controllable sources.

coefficient (R) remained unchanged but that the total phosphorus load increased proportionally with a growing human population and a growing per capita discharge of phosphorus (E_c) connected with increasing fertilizer and detergent use. From Fig. 14, it is quite evident that after 1935 the loading rate increased much faster than before. As an example, the Okanagan Lake phosphorus load increased by only 0.025 g/m² between 1900 and 1935 while during the next 35 years it increased by as much as 0.24 g/m², about 10 times more than during the previous period. If no improvement in sewage and industrial pollution treatment took place, the total load to Okanagan Lake would increase by 1990 to 0.63 g/m²·year total P, a load comparable to the present one to Lake Ontario (Anon. 1969, Patalas 1972). The corresponding 1990 figures for the remaining lakes are: 3.7-g/m²·year total P for Skaha Lake, 4.2 g for Osoyoos Lake, 0.84 g for Wood Lake, and 0.53 g for Kalamalka Lake (Fig. 14). Assuming, however, that a plan to remove 80 per cent of phosphorus from controllable sources was implemented soon enough, the phosphorus load would amount by 1990 to 0.19-g/m²·year total P for Okanagan Lake, 0.9 g for Skaha Lake, 1.5 g for Osoyoos Lake, 0.14 g for Kalamalka Lake, and 0.17 g for Wood Lake. The trend of trophic changes in lakes Okanagan and Kalamalka could then be reversed from mesotrophy to the middle range of oligotrophy; Skaha and Osoyoos lakes would change from high to moderate eutrophy, and Wood Lake from moderate eutrophy to mesotrophy, a situation that probably existed in these lakes around 1945. A further reversing of eutrophication of Skaha and Osoyoos lakes would probably require a more efficient than 80% phosphorus removal from controllable sources as well as an increasing control of the use of fertilizers in agri- and horti-culture in the Okanagan Valley.

Acknowledgments

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NOTES

Fecundity of Resident and Anadromous Dolly Varden (*Salvelinus malma*) in Southeastern Alaska

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BLACKETT, R. F. 1973. Fecundity of resident and anadromous Dolly Varden (*Salvelinus malma*) in southeastern Alaska. J. Fish. Res. Board Can. 30: 543–548.

Fecundity of resident Dolly Varden (*Salvelinus malma*) in an isolated population of southeastern Alaska averaged 66 eggs per female in comparison with 1888 eggs for anadromous Dolly Varden from two nearby streams. A relatively large egg size, averaging 3.6 mm in diameter and overlapping the range for the anadromous char, has been retained by the females in the resident population. Curvilinear regressions between egg number and fish length and linear regressions between egg number and body and ovary weights show that resident females have fewer eggs per unit of length, approximately the same number of eggs per gram of body weight, and more eggs per gram of ovary weight than anadromous females. The resident char attain sexual maturity a year earlier in life and at a smaller size than the migratory char. Development of a larger left ovary containing more eggs than the right was a common occurrence for both resident and anadromous Dolly Varden.

BLACKETT, R. F. 1973. Fecundity of resident and anadromous Dolly Varden (*Salvelinus malma*) in southeastern Alaska. J. Fish. Res. Board Can. 30: 543–548.

Les truites malma (*Salvelinus malma*) landlockées et formant une population isolée dans le sud-est de l'Alaska, produisent en moyenne 66 oeufs par femelle. Par contre, les populations anadromes de deux cours d'eau avoisinants produisent en moyenne 1888 oeufs par femelle. Les truites landlockées atteignent la maturité sexuelle un an plus tôt et à une taille plus petite que les individus anadromes. Les oeufs de la population résidente retiennent une taille relativement grande, soit 3.6 mm de diamètre moyen. La fécondité des populations landlockées et anadromes s'exprime sous forme de régressions curvilignes entre le nombre d'oeufs et la longueur du poisson, et de régressions linéaires entre le nombre d'oeufs et le poids du corps et de l'ovaire. On rencontre communément, à la fois chez les truites landlockées et chez les truites anadromes, un ovaire gauche plus développé que l'autre et contenant plus d'oeufs.

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THE fecundity of Dolly Varden (*Salvelinus malma*) was studied to obtain information on the reproductive potential of freshwater stocks, which are abundant and widely distributed throughout southeastern Alaska. Both resident and anadromous populations provide an important and increasingly popular sport fishery in the state. Fecundity of anadromous Dolly Varden from lake and stream systems was investigated in 1964 and 1965 (Blackett 1968) as one phase of intensive research by the Alaska Department of Fish and Game to formulate basic criteria for management. In 1966, fecundity data were collected from a population of resident Dolly Varden that was isolated by a 12-m falls at tidewater. The fecundity of resident Dolly Varden has not been reported previously and this is the first collation of information on fecundity of both resident and anadromous Dolly Varden stocks in southeastern Alaska.

Study area and methods — Resident Dolly Varden were collected from Falls Creek, located on the southwest portion of Admiralty Island, in the South Arm of Hood Bay (Fig. 1). The creek is approximately 2.4 km in length and originates from many small rivulets, glacier melt, and beaver pond seepage. The stream is about

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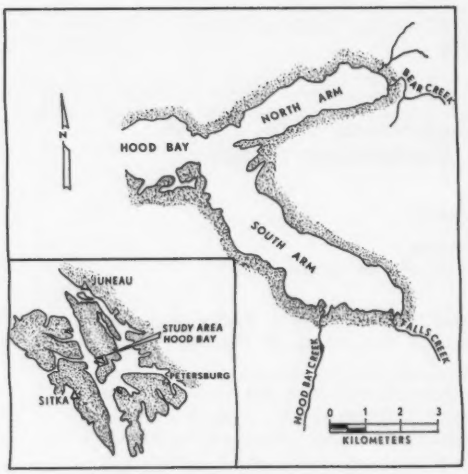

FIG. 1. Hood Bay study area on Admiralty Island, southeastern Alaska.

6–9 m wide and contains numerous shallow riffles and deep pools. The origin of the resident Dolly Varden is unknown, but most likely the population was established from a natural introduction of anadromous char. The falls at tidewater has been a barrier to anadromous fish for over a century.

Anadromous Dolly Varden had been collected previously for fecundity studies (Blackett 1968) from Hood Bay and Bear creeks, also located in the South and North arms of Hood Bay. Falls Creek is approximately 1.8 km from Hood Bay Creek and 6.4 km from Bear Creek. The three study streams are nonlake systems situated in the undeveloped wilderness of upper southeastern Alaska.

Shortly before spawning, Dolly Varden were trapped at Falls Creek in September and October by minnow traps baited with a cheesecloth sac of salmon eggs. The traps, capable of capturing fish up to 250 mm in length, were set for 2–3-day periods. As the sampling progressed, only females of a length needed to extend the data over a broader length range were kept.

The specimens were killed, measured to the nearest millimeter, and weighed to the nearest centigram, and the right and left ovaries were individually dissected from the body cavity and weighed separately to the nearest centigram. Each ovary was placed in a petri dish containing a physiological saline solution and five eggs from anterior, middle, and posterior sections dissected from the ovarian tissue. Eggs were measured with the micrometer scale of a binocular microscope. A mean egg diameter from the measurements of 10 eggs was recorded for each fish. The eggs in each ovary were then counted. Otoliths were dissected from the skull for age determination.

Anadromous Dolly Varden were collected from Hood Bay and Bear Creek by hook and line immediately before spawning in September and October of 1965. Fish were examined by methods identical to those described for Falls Creek with the exception of egg counting. Ovaries of the anadromous char were preserved in formalin and the eggs counted at a later date.

Regression equations were calculated from logarithmic transformed data to provide variance constancy. The curves were plotted from logarithmic values converted to natural numbers.

Results — The resident Dolly Varden at Falls Creek were smaller than the anadromous Dolly Varden from Hood Bay and Bear creeks and produced fewer eggs per female (Table 1). The largest mature char taken from Falls Creek was only 207 mm in fork length while the smallest mature anadromous female was 295 mm long. Average fecundities were 66 and 1888 eggs per female and 4.1 and 3.0 eggs per gram of body weight for the resident and anadromous char, respectively. Eggs of the resident fish were relatively large, averaging 3.6 mm in diameter, and in some specimens were even larger than eggs of the anadromous females.

The resident char in Falls Creek matured at an earlier age than anadromous Dolly Varden. A few resident females (11%) had attained maturity at age 3 and the majority (53%) were mature in the fourth year of life. The oldest fish collected from Falls Creek was age 7. Anadromous Dolly Varden obtained by hook and line were predominantly age 6 and 7 (72%) and the oldest female was age 10. Samples collected by hook and line from Hood Bay and Bear creeks were considered somewhat selective of older fish as most of the anadromous potential spawners in these systems were age 5 and 6 (Armstrong and Winslow 1968).

Comparison of fork length–fecundity regression curves and equations (Fig. 2) indicates substantially fewer eggs per millimeter of length for the resident than for the anadromous char. Curvilinearity of the regressions for the two groups appears similar.

Analysis of covariance indicated a significant difference ($P = 0.01$) in elevation (average log of fecundity adjusted to a common log of body length) but not in slope (relative rate of increase in fecundity per unit of length) of the length–fecundity regressions of the resident and anadromous char. An assumption of analysis of covariance that samples were drawn from normal populations with homogenous variance is considered satisfied as heterogeneous variance was not evident from the mean squares of the transformed data.

Linear regressions expressing the relation between fecundity and body weight (Fig. 3) were similar for the anadromous and the resident char. The Bear Creek sample had a greater regression

TABLE 1. Average fecundity measurements and ranges (parenthesis) of anadromous and resident Dolly Varden (*Salvelinus malma*) from southeastern Alaska.

Sample area	Sample size	Fork length (*mm*)	Body weight (*g*)	Eggs per female	Eggs per mm body length	Eggs per g body weight	Egg diameter (*mm*)	Ovary weight (*g*)	
								Left	Right
Anadromous									
Hood Bay Creek	66	383 (301–498)	635.03 (317.51–1315.41)	1846 (739–3086)	4.8 (2.2–6.9)	2.9 (1.4–5.1)	4.4 (3.0–5.6)	48.29 (10.95–133.20)	47.64 (10.11–151.33)
Bear Creek	59	385 (295–480)	635.03 (226.79–1224.69)	1931 (752–4232)	4.9 (2.6–9.6)	3.1 (2.1–4.1)	4.7 (3.4–5.4)	52.81 (8.17–123.21)	51.16 (9.28–137.31)
Resident									
Falls Creek	55	114 (91–207)	17.32 (8.70–95.46)	66 (38–212)	0.6 (0.4–1.0)	4.1 (2.2–6.4)	3.6 (2.9–4.3)	0.94 (0.34–5.07)	0.88 (0.37–4.51)

slope than either of the other samples. The regression slope for the resident char is thought to be more representative of the fecundity–weight relation than the average number of eggs per gram.

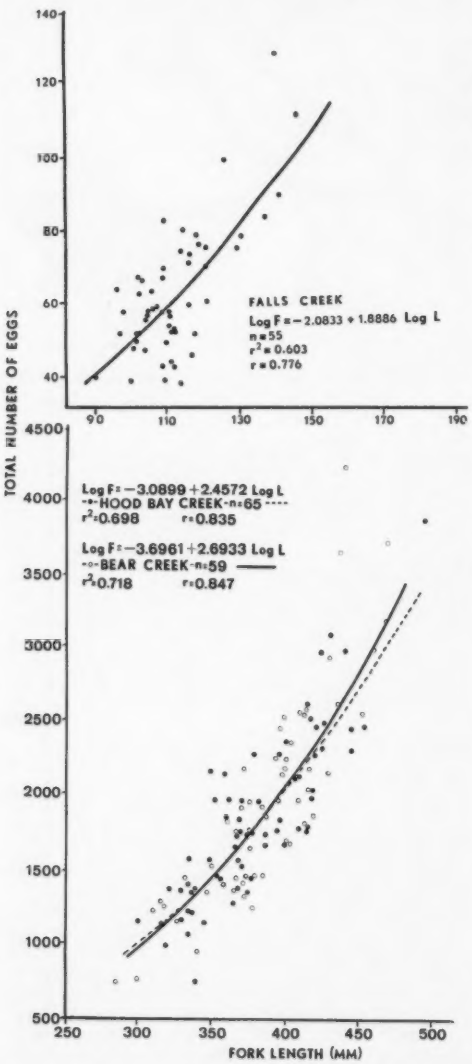
TOTAL NUMBER OF EGGS
FALLS CREEK
Log F = −2.0833 + 1.8886 Log L
n = 55
r² = 0.603
r = 0.776
Log F = −3.0899 + 2.4572 Log L
HOOD BAY CREEK n=65
r²=0.698 r=0.835
Log F = −3.6961 + 2.6933 Log L
BEAR CREEK n=59
r²=0.718 r=0.847
FORK LENGTH (MM)

FIG. 2. Fecundity relation to fork length of resident (top) and anadromous (bottom) Dolly Varden (*Salvelinus malma*). The falls Creek sample had one resident fish with 212 eggs and a length of 208, which is included in regression analysis, but not shown on the graph.

The regressions relating ovary weight to body weight and fecundity for the resident and anadromous char (Fig. 4, 5) indicate greater similarity for ovary weight–body weight than for fecundity–ovary weight. The resident char had an average of 17 more eggs per gram of ovary weight than the anadromous Dolly Varden, probably due to fewer eggs with less ovarian tissue contributing to the ovary mass. The progressive increase in ovary weight during maturation of ova in relation to total body weight provides a means of indexing maturity and determining spawning period (Blackett 1962, 1968). Ovary weight regressions are also useful

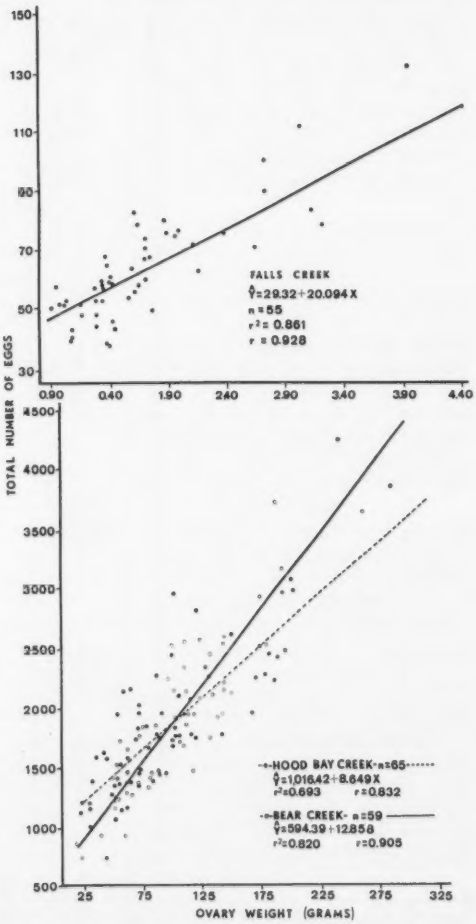

FIG. 3. Fecundity relation to body weight of resident (top) and anadromous (bottom) Dolly Varden.

indicators of fecundity and rate of maturation when actual examination and counts of eggs are impractical.

Of 179 female Dolly Varden examined, 59.9% had a larger left ovary containing more eggs than the right ovary. The larger left ovary was characteristic of both the anadromous and resident char. However, a Student's *t*-test indicated that for paired measurements of the samples the difference

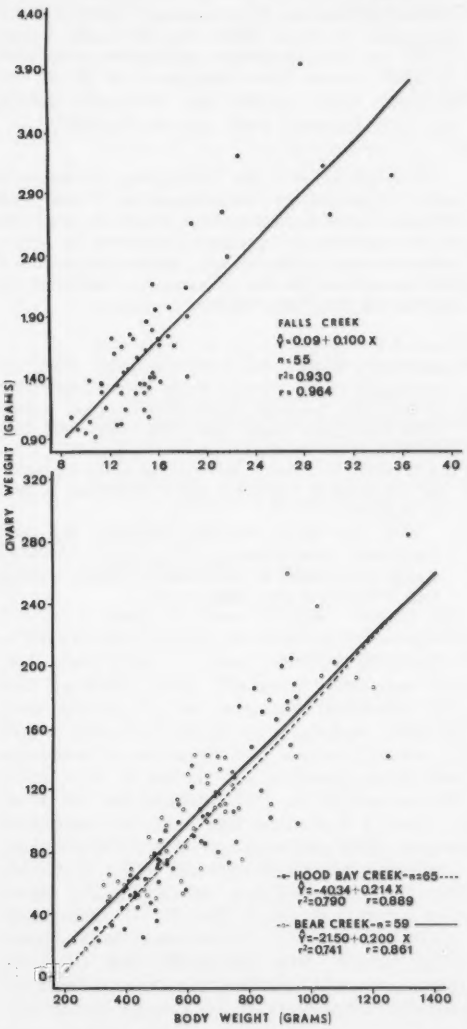

FIG. 4. Relation between body weight and ovary weight of the resident (top) and anadromous (bottom) Dolly Varden at onset of spawning. The sample of resident Dolly Varden from Falls Creek had one fish with a weight of 95.46 g and an ovary weight of 9.58 g, which is included in regression analysis, but not shown in the graph.

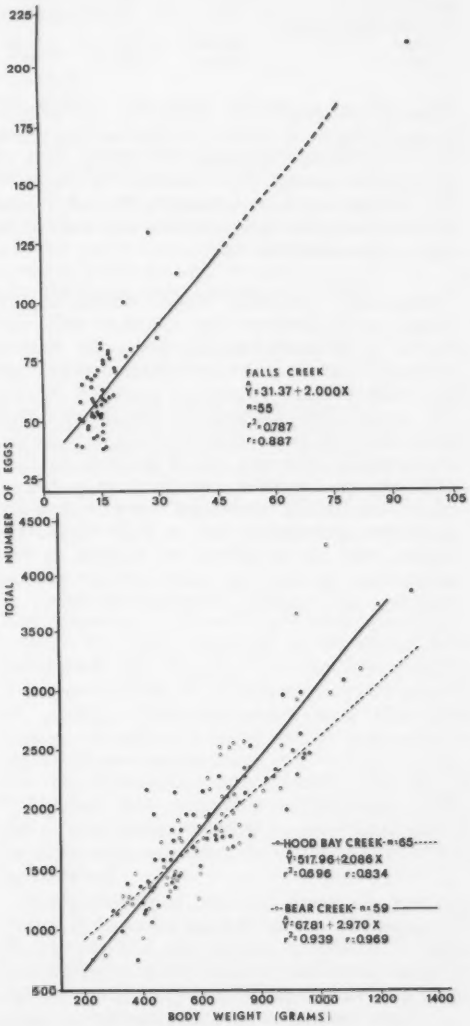

FIG. 5. Fecundity–ovary weight relation of the resident (top) and anadromous (bottom) Dolly Varden immediately before spawning. The Falls Creek sample had one resident fish with 212 eggs and an ovary weight of 9.58 g, which is included in regression analysis, but not shown on the graph.

was not significant ($P = 0.05$), the average numbers of eggs being:

	Anadromous		Resident
Creek	Hood Bay	Bear	Falls
Sample size	65	59	55
Average number eggs			
Right	913.0	950.3	32.0
Left	931.8	981.2	34.0

Although not statistically significant, a disproportionately larger left ovary is a common occurrence for Dolly Varden spawning in some systems in southeastern Alaska. This condition of the ovary was determined to be significant ($P = 0.02$) for anadromous Dolly Varden from a lake and coastal river system (Blackett 1968).

Discussion — Fecundity studies conducted previously on anadromous char (Blackett 1968) also showed a different fecundity–body size relation for populations sampled from lake, coastal river, and inland stream systems of southeast Alaska. The reproductive potential of the resident char (assuming an equivalent number of female spawners) is considerably less than that of anadromous char. This reduced fecundity may serve as a natural mechanism limiting population size in a restricted freshwater environment such as Falls Creek. The resident char are thought to be adapted to their environment by small size, early maturity, reduced fecundity, and, possibly, shortened life span.

The remarkably large egg size of the Falls Creek char in relation to fish size and egg number is noteworthy. If these resident char originated from anadromous Dolly Varden, then the large egg size was retained while fish size and, in turn, egg number was greatly reduced during development of this isolated population. It is suspected that this condition exists in many other resident Dolly Varden stocks and that freshwater populations established in small streams from transplants or fry of anadromous Dolly Varden may eventually develop fish with decreased body size and fecundity.

Acknowledgments — This investigation was supported with Federal Aid in Fish Restoration Funds under Project F-5-R-7. I am grateful to Mr R. H. Armstrong for his assistance and guidance throughout the project, and to the Sport Fish Division, Alaska Department of Fish and Game, for the opportunity to conduct this research on the Dolly Varden.

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Spontaneous Nephroblastoma in a Rainbow Trout (*Salmo gairdneri*)[1]

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ODENSE, P. H., V. H. LOGAN, AND S. R. BAKER. 1973. Spontaneous nephroblastoma in a rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 549–551.

A neoplasm in a rainbow trout (*Salmo gairdneri*) identified as a nephroblastoma is described and its possible pathological implications discussed. The characteristic conditions of abortive renal tubules and glomeruli in a fibrous stroma were observed; however, metastases were absent. The simultaneous presence of inflammatory kidney disease made association of clinical signs with the neoplasm impossible. This is the first case of nephroblastoma in Canadian hatchery stock. The etiological factors are unknown.

ODENSE, P. H., V. H. LOGAN, AND S. R. BAKER. 1973. Spontaneous nephroblastoma in a rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 549–551.

Les auteurs décrivent un néoplasme observé chez la truite arc-en-ciel (*Salmo gairdneri*), qu'il identifient comme étant un néphroblastome. Ils en discutent les implications pathologiques possibles. Ils notent les conditions caractéristiques des tubules et des glomérules rudimentaires du rein; cependant, il n'y a pas de métastases. Par suite de la présence simultanée d'une maladie inflammatoire du rein, il a été impossible d'associer symptômes cliniques et néoplasme. Il s'agit du premier cas de néphroblastome chez un stock d'élevage au Canada. On n'en connaît pas l'étiologie.

Received October 26, 1972

THE term nephroblastoma (Wilms' Tumor) describes a morphologically mixed embryonic neoplasm that arises from the renal blastema (Hottendorf and Ingraham 1968). The many terms that have been applied to this neoplasm (Feldman 1928; Willis 1961; Hottendorf and Ingraham 1968) are considered synonomous and nephroblastoma appears to be in current use. Although nephroblastomas are not common, they are phylogenetically widespread and have been reported in a variety of mammals (Hottendorf and Ingraham 1968), chickens (McKenny 1931), and amphibians and fish (Harshbarger 1972). Ghittino and Dalforno (1971) and Harshbarger (1972) each briefly described a cryptogenic nephroblastoma in a rainbow trout (*Salmo gairdneri*) and Helmboldt and Wyand (1971) described a case in a striped bass (*Morone saxatilis*). The authors emphasized the characteristic abortive development of glomeruli and tubules in a fibrous stroma. The lesion described in the striped bass (Helmboldt and Wyand 1971) was interesting in that approximately 90% of the tumor was composed of cartilage. Nephroblastomas have also been induced in rainbow trout by feeding diets containing N-nitrosodimethylamine and by injecting fish, less than 1-year-old, intraperitoneally with 100 μc I^{131} (Ashley 1970). According to Harshbarger (1972), the induced lesion appeared to grow faster and to be more anaplastic than the cryptogenic case that he described.

Nephroblastomas have not previously been reported in Canadian hatchery stocks. The paucity of descriptions and the apparent possibility of inter- and intraspecific differences in nephroblastomas of fish prompt us to present this description of a spontaneous nephroblastoma in a rainbow trout.

Materials and methods — During regular culling of brood stock at a commercial fish culture station in March, 1972 a rainbow trout was observed swimming on its side. The specimen was scoliotic, which warranted its removal. Externally, other than the scoliosis, the speci-

[1]Samples of this tumor have been placed in the collection of The Registry of Tumors in Lower Animals, Smithsonian Institution, United States National Museum Washington, D. C. 20560, accession number RTLA 673.

Printed in Canada (J2711)

men appeared in excellent condition. It was a female, 51 cm in length, weighing 0.9 kg.

The fish was obtained as a fingerling in 1969 and during 1969 and 1970 it received several chemotherapeutic treatments including Diquat (10–30 ppm), malachite green (1 ppm), terramycin (30 g/100 lb fish/day), sulfamethazine (5 g/100 lb fish/day), and nitrofuran (30 g/100 lb fish/day). The fish had also been anesthetized with MS 222 (tricane methanesulfonate) during spawning. Chemotherapy was discontinued in November 1970.

At necropsy, a greyish-white neoplastic growth was observed replacing approximately the posterior 4.5 cm of the hind kidney. The tumor was removed and fixed in 10% formalin. Liver, midkidney, spleen, stomach, intestine, pyloric caeca, gill, and muscle (near the tumor) were also removed for histological examination. Paraffin sections were stained with hematoxylin and eosin and Mallory's triple connective tissue stain.

Results — Gross — At necropsy, an excessive discharge of biliverdin was indicated by the green color of the bile duct, pyloric caeca, and intestine. A Gram's smear of the midkidney indicated inflammatory kidney disease (*Corynebacterium* sp.).

The lobulated tumor (Fig. 1) measured approximately $4.5 \times 3.5 \times 1.7$ cm, being rounded dorsally and flattened ventrally. It was firm and pushed the swimbladder slightly ventrally. The growth was surrounded by a connective tissue coat and did not appear to infiltrate the dorsal musculature (Fig. 2). It was, however, difficult to separate from normal renal tissue. The peritoneum appeared intact and normal but the whorls of neoplastic tissue were visible beneath it. Hemorrhage in host tissue and within the neoplasm was not visible on gross examination. Dark tissue, characteristic of normal kidney tissue, was observed peripherally, especially dorsally, and occasionally small bands went deep into the tumor mass. When bisected some areas of the neoplasm appeared cystic (Fig. 2).

Microscopic — The tumor was separated from the muscle by a connective tissue band (Fig. 3) but there was some fibrosis in the muscle and edema and atrophy of the muscle fibers, indicating compression by the tumor. Fibrous bands also separated the tumor from normal renal parenchyma (Fig. 4) so that the overall appearance of the tumor was that it was well defined from adjacent normal tissues rather than being highly invasive. Bands of normal renal tissue were observed extending deep into the tumor (Fig. 4). Hyperemia and hemmorhage were observed in many areas but were more prevalent in the connective tissue bands near the periphery of the tumor.

The tumor consisted of the usual mixture of connective and epithelial tissues with attempted renal tubule and glomerular formation (Fig. 5). The cells of the sarcomatous portion (Fig. 6) were round to fusiform. The nuclei were large, ovoid to vesicular, with a distinct nuclear membrane and diffuse chromatin. The nucleolus was small and usually central. Mitotic figures were readily found and focal necrosis was common.

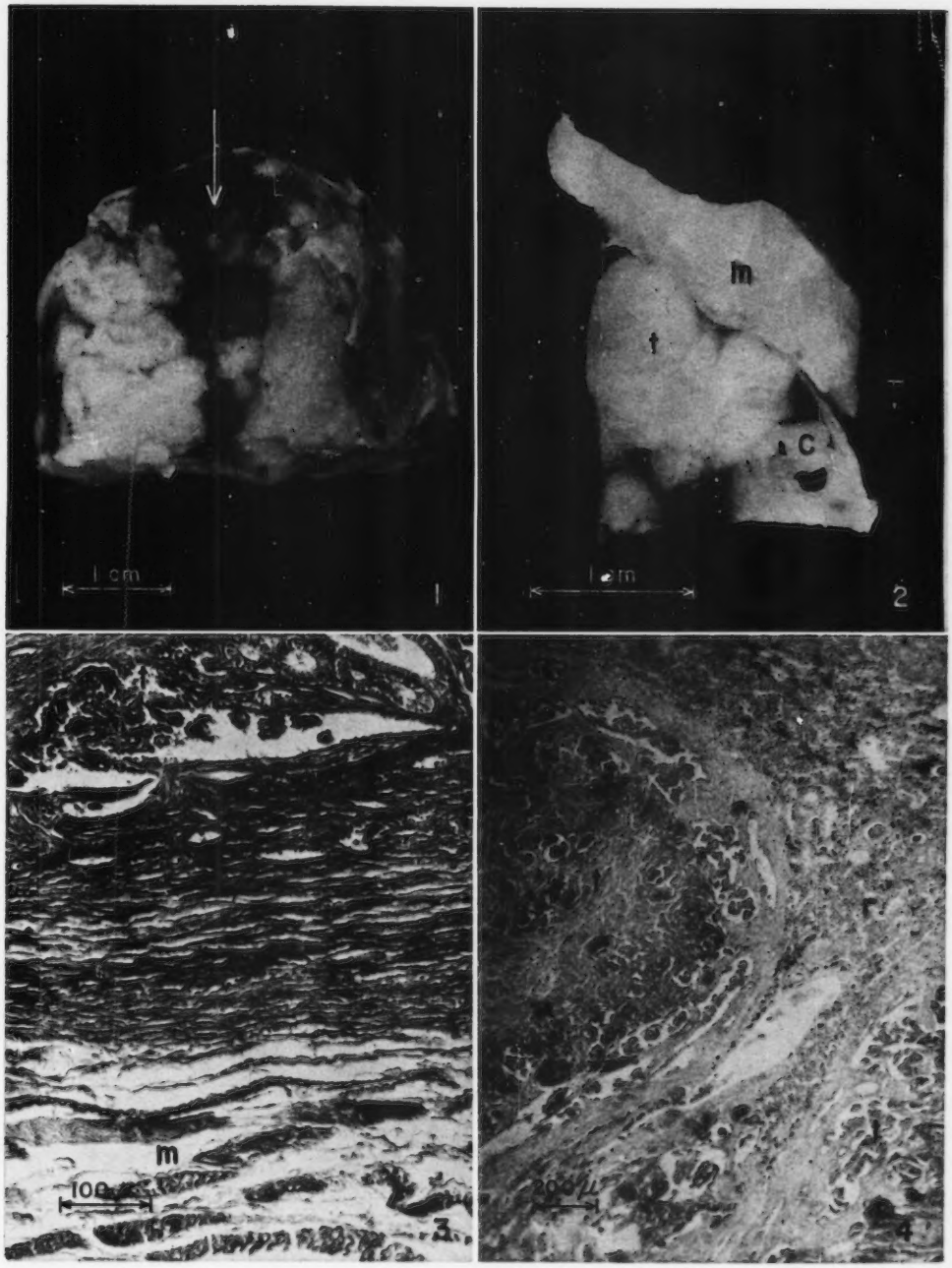
The adenomatous element consisted of islands of basophilic epithelial cells, cuboidal to flattened, with an ovoid, hyperchromatic nucleus and small, dark, central nucleolus. As these cell groups differentiated further, abortive renal structures developed. In some zones, epithelial structures were particularly prominent and well developed tubules and glomeruloid structures were present near the collagenous septa (Fig. 7). The pseudoglomeruli (Fig. 8) were usually surrounded by flattened cells giving the appearance of a capsular space. The cells of the glomerular tuft were cuboidal or flattened while those of the renal tubules ranged from low columnar or cuboidal with hyperchromatic oval nuclei to columnar with pale vesicular nuclei (Fig. 8). Most tubules, or groups of tubules, were surrounded by a layer of cuboidal or flattened cells. Hematopoeitic tissue and melanin pigment were not observed. Cystic structures were common.

Metastases to liver, midkidney, spleen, stomach, intestine, pyloric caeca, gill, and muscle were not observed.

Discussion — This nephroblastoma, the first case recorded in Canadian hatchery stock, exhibits the characteristic attempted development of glomeruli and tubules from a background of neoplastic mesonephric mesenchyme. The lesion resembles those described by Ashley (1970), Ghittino and Dalforno, (1971) and Harshbarger (1972) but differs from some mammalian nephroblastomas and that described by Helmboldt and Wyand (1971) in that stromal metaplasia was not a prominent feature. The amount of fibrous material was greater than in the cryptogenic case described by Harshbarger (1972) but less than in the cases induced by Ashley (1970) with nitrosamines (Harshbarger personal communication).

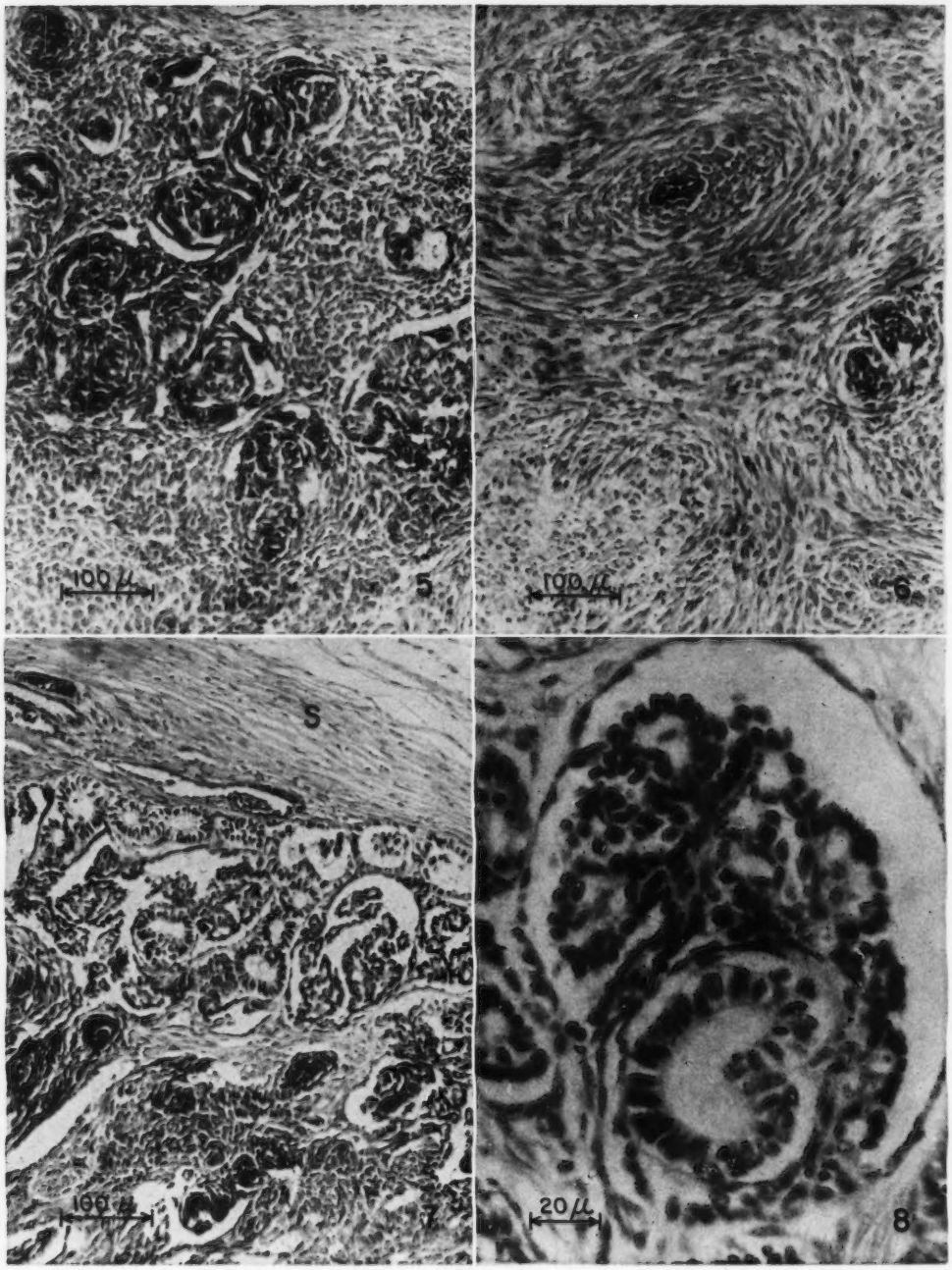
The tumor was confined and grew only by expansion. The firm attachment to surrounding normal renal tissue was due to the bands of normal renal tissue being enveloped but not infiltrated by the tumor.

The chemotherapeutic agents used are not known to have carcinogenic effects, industrial pollution in the area is negligible and, although the natural distribution of nitrosamines is not known (Harshbarger 1972), it must be stated that the etiological factor(s) are unknown but were apparently at a low level since only one case occurred in a group of more than 350 rainbow trout examined.



FIGURES 1–4

FIG. 1. Dorsal view of the excised tumor. Note the lobulated appearance and the presence of normal renal tissue (arrow). FIG. 2. A half transverse section of the tumor and associated body muscle. The connective tissue layer is visible between the muscle (m) and tumor (t). An apparent cystic formation (c) is also present. FIG. 3. The thick connective tissue layer separating the tumor (t) from the muscle (m). There is muscle fiber atrophy and fibrosis. Mallory's triple connective tissue stain. FIG. 4. Band of normal renal tissue (r) extending between two lobules of the tumor (t). Note the distribution of melanin pigment in the kidney tissue and the layer of connective tissue separating the tumor from the kidney tissue. H and E.



FIGURES 5–8

FIG. 5. A primarily adenomatous portion of the tumor. Note the variation in degree of differentiation of glomeruloid structures and tubules. H and E. FIG. 6. A sarcomatous portion of the tumor. A necrotic focus is visible in the lower left. H and E. FIG. 7. A primarily adenomatous portion of the tumor. Note the highly developed tubules near a major stromal septum (s). H and E. FIG. 8. Developing pseudoglomerulus and tubules. H and E.

In mammals the most important factor in longevity is the presence or absence of metastases rather than renal disfunction (Boyd 1970). The only previous mention of the possible pathological implications of these lesions on fish was the suggestion by Helmboldt and Wyand (1971) that the lesion did not affect the fighting ability. The position of the fish kidney, especially at the posterior pole, places these tumors in contact with the backbone. Thus, in some cases, the possibility of a pressure effect on the nerves and muscle cannot be excluded. Pressure atrophy of muscle near the tumor was indicated in the present study. However, the presence of inflammatory kidney disease prevents us from relating the erratic swimming behavior of this specimen directly to the neoplasm.

The slight effect of the neoplasm on the normal renal tissue would not result in any apparent disfunction. The peripheral hemorrhage observed in the present study was also noted by Ashley (1970). If extensive enough it could presumably result in an anemic condition. However, the excessive discharge of biliverdin observed in this specimen resulted from hemorrhage in the midkidney due to kidney disease rather than the neoplasm.

Acknowledgments — We wish to thank Dr R. MacKelvie, Fisheries Research Board of Canada, Halifax Laboratory, Halifax, N.S., and Dr. C. Frantsi, Fisheries Service, Federicton, N. B., for their confirmatory diagnosis of *Corynebacterium* sp.; Dr J. C. Harshbarger, Registry of Tumors in Lower Animals, Museum of Natural History, Smithsonian Institute, Washington, D.C., for his helpful discussion; and Dr G. Fraser, Assistant Director, Pathology Institute, Halifax, N.S., for his helpful advice and criticism.

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Diel Migration and Breeding Cycle of *Aglantha digitale* from Two Locations in the Northeastern Pacific

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ARAI, M. N., AND J. FULTON. 1973. Diel migration and breeding cycle of *Aglantha digitale* from two locations in the northeastern Pacific. J. Fish. Res. Board Can. 30: 551–553.

The trachymedusa *Aglantha digitale* undergoes a diel migration in Saanich Inlet, Vancouver Island, British Columbia. The species has a single yearly breeding cycle at a high seas station in the northeastern Pacific.

ARAI, M. N., AND J. FULTON. 1973. Diel migration and breeding cycle of *Aglantha digitale* from two locations in the northeastern Pacific. J. Fish. Res. Board Can. 30: 551–553.

La trachyméduse *Aglantha digitale* subit une migration nycthémérale dans l'inlet Saanich, île Vancouver. A une station de haute mer du Pacifique Nord-Est, cette espèce a un seul cycle reproducteur par année.

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Aglantha digitale (O. F. Müller 1776) is a trachymedusa with a circumpolar distribution (Kramp 1947, 1959, 1965). A number of authors have recorded its presence in the waters off the west coast of Canada (see Shih et al. 1971 for references). This note describes two observations more pertinent to the general biology of the species. The first shows diel migration in a coastal inlet; the second shows the annual life cycle and the size-classes at a high seas station.

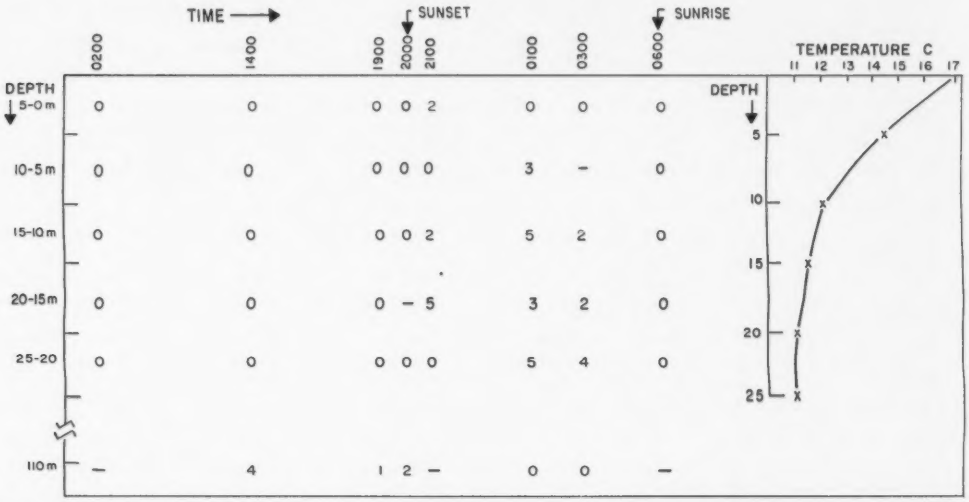

FIG. 1. Number of *Aglantha digitale* (7–13-mm bell height) per 10 m³ of water at depths indicated showing diel migration. Sunset and sunrise are indicated by arrows. Temperature plotted for 1900 hr. Salinity 29.0–29.9‰. Saanich Inlet, August 31–September 1, 1965.

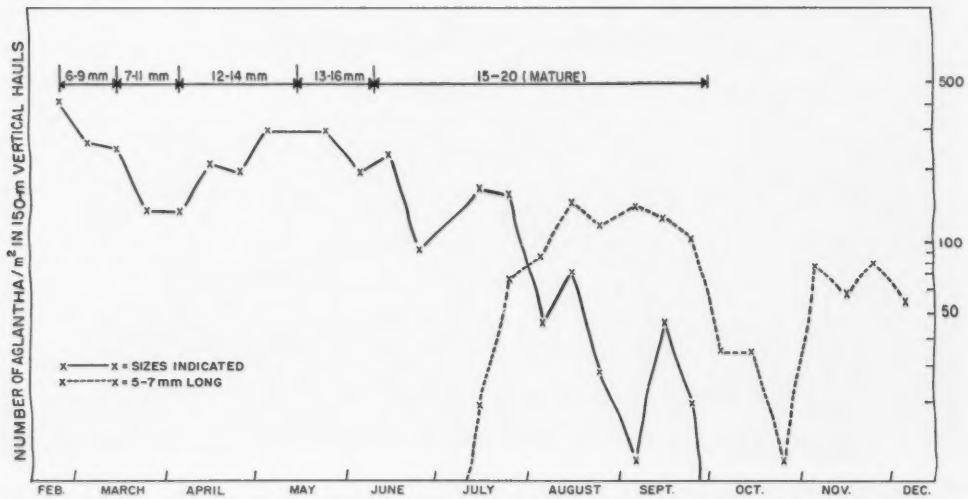

FIG. 2. Number of *Aglantha digitale* in 150-m vertical hauls expressed as the 10-day mean of the number per square meter (total volume of each haul was 37.5 m³). No animals less than 15-mm bell height were sexually mature.

Diel migration — Plankton samples were collected in Saanich Inlet, Vancouver Island, British Columbia, over a 24-hr period August 31–September 1, 1965, using Clarke-Bumpus samplers with 350-μ mesh netting. The samplers were towed at 1–1.5 m/sec obliquely at 5-m intervals, sampling the upper 25 m. Each net filtered approximately 10 m^3 of water. An additional sampler was towed at approximately 110 m. The total depth of the inlet is 200 m. Care was taken to sample 1 hr before sunset, at sunset, and 1 hr after sunset as well as 1 hr before, at, and after sunrise so that the effect of changes in light intensity on vertical migration could be noted. Temperature and salinity measurements of the upper 30 m were taken every 8 hr during the series using an in situ salinometer. Throughout the series the air was calm and the sea surface was smooth.

Figure 1 shows diel migration of *A. digitale* into the upper water layers of Saanich Inlet. The chaetognath *Sagitta elegans*, the euphausiid *Euphausia pacifica*, and the copepod *Metridia pacifica* showed the same pattern of migration, but *Calanus pacificus* remained near the surface during the day.

This is the first record of complete diel migration of *Aglantha*. Hansen (1951) found that *Aglantha* migrated towards the surface at night in Oslo fjord but were stopped by a discontinuity layer at approximately 10 m, where the temperature increased from 7 to 19 C and the salinity decreased from 33 to approximately 20‰. In Saanich Inlet there was no halocline and the thermocline was only 6 C. However, Russell (1925) sampled over an 18-hr period off Plymouth, England, and concluded that *Aglantha* showed little or no migration at night although a thermocline of only 2 C existed. McLaren (1969) sampled Ogac Lake, a landlocked fjord on Baffin Island, and found no upward vertical migration at night although the peak of the concentration for *Aglantha* was well below the thermocline and halocline.

Life cycle — Plankton samples were collected daily (weather permitting) February–December 1971 from Ocean Weather Station "P" (50°N, 145°W) with a 0.25-m^2 mouth-opening cylinder-cone sampler of 350-μ black nitex netting. Hauls were made from 50 m to surface and from 150 m to surface at 1 m/sec usually at 0830 local time.

In July, juvenile *A. digitale* (5–7-mm bell height) were at a concentration of about 1/m^3 in 150-m hauls (Fig. 2). They grew to 6–9 mm by December and the decreasing concentration probably indicated that some of the population lived below 150 m. By spring they returned to the upper layers and reached a concentration of 2/m^3. Growth and maturation continued until mid-July when the maximum size of 15–20 mm was reached and reproduction occurred. This was followed by a marked decrease in numbers of large animals. Gonad vs. size data was not obtained but gonads were not seen in animals less than 15-mm bell height.

These data show a single generation per year at Station "P". Kramp (1927) postulated a single generation per year in the Kattegat and North Sea based on maximum abundance of small animals in early summer. However, off Plymouth Russell (1938) found at least three generations of small (5–7 mm) sexually mature animals in the summer followed by overwintering animals that became 12–18 mm high before spawning. In the present population small animals were not sexually mature. The rapid disappearance of large animals in August correlated with the appearance of young animals indicates, therefore, a single short breeding season in July and August in a high seas population.

Acknowledgments — Open ocean samples were collected by members of the Marine Science Branch of the Department of Energy, Mines, and Resources, Victoria, B.C., and the Saanich Inlet samples were collected by the members of the Environmental Research Group of the Fisheries Research Board, Nanaimo, B.C.

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Notes on the Whitefish of the Colville River, Alaska

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ALT, K. T., AND D. R. KOGL. 1973. Notes on the whitefish of the Colville River, Alaska. J. Fish. Res. Board Can. 30: 554–556.

Five whitefish species are present in the Colville River. Least cisco (*Coregonus sardinella*) was the most common species in the Colville Delta, while the broad whitefish (*C. nasus*) was most abundant at test net sites near Umiat.

Limited age and growth data indicate slower growth than in interior Alaska waters.

ALT, K. T., AND D. R. KOGL. 1973. Notes on the whitefish of the Colville River, Alaska. J. Fish. Res. Board Can. 30: 554–556.

On trouve cinq espèces de corégones dans la rivière Colville. Le cisco sardinelle (*Coregonus sardinella*) est l'espèce la plus commune dans le delta, alors que le corégone tschir (*C. nasus*) prédomine sur les lieux de pêche expérimentale au filet près d'Umiat.

Le peu de données que nous ayons sur l'âge et la croissance indiquent une croissance plus lente que dans les eaux de l'intérieur de l'Alaska.

Received July, 1972

THE 1968 oil discoveries on Alaska's North Slope prompted the Alaska Department of Fish and Game, Sport Fish Division, to initiate fish studies in this area. This report presents whitefish data collected during the 1970 summer Colville River survey.

Five species of whitefish, *Coregonus* sp. *sensu latu*, are the most common fish inhabiting rivers draining into the Arctic Ocean from the North Slope of Alaska. Previous research on North Slope whitefish has consisted of age and growth studies of round whitefish (*Prosopium cylindraceum*) and least cisco (*Coregonus sardinella*) at Point Barrow (Wohlschlag 1954; Cohen 1954), as well as taxonomic and distribution studies (Walters 1955; Lindsey 1962).

A commercial fishery operating in the Colville River Delta since 1950 annually takes approximately 3000 broad whitefish (*C. nasus*) and 1000 humpback whitefish (*C. pidschian*) during the summer fishery and 20,000 *C. sardinella* and 40,000 Arctic cisco (*C. autumnalis*) in the fall fishery.

Materials and methods — Fish were collected by beach seine, rotenone, and 125 × 6 ft gillnets of five monofilament panels from ½- to 2½-inch bar mesh. The selected samples of the total catch used for age analysis and maturity status do not represent numerical strength of the various age groups.

Gillnets used by the summer commercial fishery in the Colville Delta are 5-inch stretch mesh while the winter fishery uses 3-inch stretch mesh.

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In the laboratory, gill raker counts were made on the first excised left arch with the aid of a binocular microscope. Lateral line scale counts were also made on preserved fish and included all scales with lateral line pores.

Results — Test netting operations were conducted in the Colville Delta (Fig. 1) from July 2 to July 11 and in the vicinity of Umiat from June 2 through September 6. Least cisco were the most abundant whitefish taken during July gillnet test fishing in the various channels of the Colville River Delta (Table 1). Test netting throughout the summer in the Umiat area indicated no Arctic cisco or least cisco had passed through the area by September 6, when netting was terminated (Table 2). Broad whitefish predominated in the catch at Umiat. Beach seining in various locations in the Colville River Delta in July took fry and immature fish of all five species of whitefish.

Broad whitefish — The broad whitefish is easily separable from the humpback whitefish by its short gill rakers and short rounded snout (Lindsey 1962). Meristic counts for Colville River fish were: gill rakers, 19–22 ($\bar{x} = 20.1$, $n = 15$); lateral line scales, 81–90 ($\bar{x} = 84.4$, $n = 8$).

Sixty-nine of the broad whitefish taken in the Delta were sampled (length range = 105–630 mm, $\bar{x} = 375$ mm). Thirty-seven percent were potential spawners. A sample of 153 fish from the Colville at Umiat was 335–670-mm fork length ($\bar{x} = 530$ mm) and composed of 86% potential spawners.

Broad whitefish feed mainly in the brackish water of the Colville Delta. The fish move upstream in small groups and the run is spread over several months with a peak in late July. It is suspected that they spawn in September in the upper Colville.

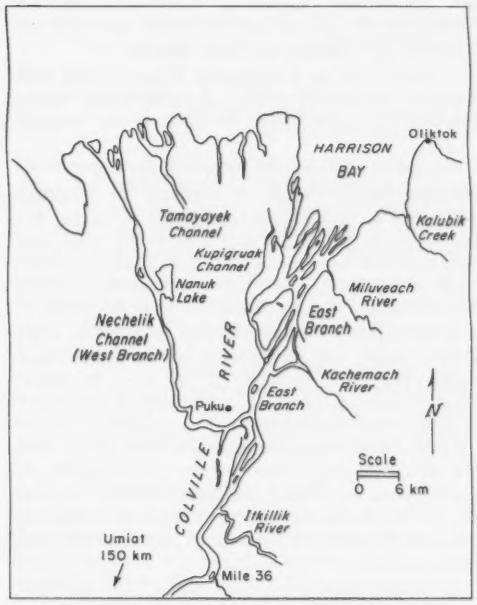

FIG. 1. Colville River Delta, Alaska.

Little is known concerning their wintering grounds but none are taken in the winter commercial fishery in the Colville River Delta.

Broad whitefish sampled in the Colville River ranged from age 0 to XV. They are slower growing than broad whitefish from more southerly waters, reaching a length of 39 cm at age VIII while Minto Flats fish (interior Alaska) are 50–55 cm at that age (Alt unpublished data). Age at maturity for the Colville sample was VII and VIII.

The commercial fishery in the Colville River Delta takes approximately 3000 broad whitefish per year averaging 2.3 kg in weight and 55 cm in length.

Humpback whitefish — The taxonomy of the Alaskan humpback whitefish has yet to be resolved but the designation of *C. pidschian* (Gmelin) is currently used. Colville River fish taken in 1970 had 20–23 gill rakers (mode = 22, $n = 15$) and 76–86 lateral line scales ($\bar{x} = 82.5$, $n = 11$).

Forty-four fish from the Colville Delta ranged from 120 to 430 mm ($\bar{x} = 345$ mm) with 37% potential spawners while the Umiat sample of 105 fish ranged from 345 to 420 mm ($\bar{x} = 380$ mm) and contained 100% potential spawners.

Humpback whitefish first appeared in the test fishery at Umiat in late July and the run peaked in mid-August. These fish presumably spawn in the upper Colville River in the fall.

The spawning population is composed of fish from age VIII to X. By comparison, Chatanika River humpback whitefish (interior Alaska) reach sexual maturity at age IV and V at 310–350 mm in length (Alt unpublished data).

TABLE 1. Whitefish gillnet catch, Colville River Delta, 1970.

Location	July	Net nights	Species captured[a]				
			LCi	ACi	BWF	HWF	RWF
Colville River–Mile 36	2	2	9	–	5	1	1
Itkillik River mouth	2,11	4	15	4	18	4	–
Putu	2,11	1	5	9	1	–	–
Nanuk Lake	4	1	32	22	21	29	4
Tamayayak Channel	6	3	16	14	27	25	–
Kachemach River	7	3	1	–	8	4	1
Miluveach River	8	1	2	–	3	–	5
Kalubik Creek mouth	9	3	207	27	15	12	3
Oliktok	9	1	10	11	–	2	–
East Branch–8 mile	10	1	1	1	–	2	–
Kupigruak Channel	10	1	2	1	10	3	–
Total			300	89	108	82	14

[a]LCi, least cisco; ACi, Arctic cisco; BWF, broad whitefish; HWF, humpback whitefish; RWF, round whitefish.

TABLE 2. Whitefish gillnet catch, Colville River at Umiat, 1970.

Month	Net hours	Species captured[a] BWF	HWF	RWF
June	480	23	–	3
July	432	84	15	4
Aug.	796	102	106	7
Sept.	11	1	–	–
Total	1,730	210	121	14

[a]BWF, broad whitefish; HWF, humpback whitefish; RWF, round whitefish.

Humpback whitefish comprise only about 1% of the winter whitefish commercial catch and about 10% of the summer catch in the Colville Delta.

Arctic cisco — Arctic cisco from the Colville River have 41–45 gill rakers (15–16 + 26–29, $n = 11$). It is the least fluvial of the whitefish and has been taken in the Beaufort Sea with salinity over 30‰.

The mean length of 58 cisco sampled from the Colville Delta catch was 300 mm (125–355 mm). Age-groups I through V were represented and all fish were immature. None were taken in the test fishery at Umiat and it is suspected that spawners enter the Colville Delta later in the summer and spawn in the lower reaches of the rivers similar to the situation in Siberia (Berg 1948). Rearing Arctic cisco were taken by seine in the Colville Delta in 1970.

The Arctic cisco comprises approximately 60–70% of the winter commercial catch in the Delta. Its fine flavor and high oil content make it a more valuable fish than the least cisco. The fishery annually takes 30,000 to 50,000 Arctic cisco averaging 0.45 kg.

Least cisco — The least cisco is often found in association with the Arctic cisco but is generally more abundant in waters with lower salinity. Gill raker counts for Colville River least cisco range from 41 to 47 ($\bar{x} = 44$, $n = 10$).

A sample of 100 least cisco taken in the Colville Delta ranged from 115 to 360 mm ($\bar{x} = 280$ mm) in length and from I to VIII in age. Seventy-five were potential spawners. Maturity is first reached at age IV and V at 220-240 mm. No least cisco were taken at Umiat. No information on its spawning in the Colville is available. The winter commercial fishery takes approximately 20,000 annually averaging 0.4 kg.

Round whitefish — The round whitefish is abundant in the upper reaches of the Colville River and is found in most of its tributary streams. One hundred nineteen round whitefish taken in the Kiruktagiak River, a Colville tributary, were 80–440 mm in length ($\bar{x} = 241$ mm). Age of these fish was not determined. Spawning occurs in tributary streams in the fall and rearing round whitefish are taken in the summer in these streams.

A section of the Kiruktagiak River treated with rotenone on July 27 yielded 12 kg of round whitefish per acre. The round whitefish is not utilized.

Discussion — With the increased development of Alaska's North Slope, an increase in whitefish utilization is expected to occur. Sport fishing for whitefish has potential, but methods for their capture have not been perfected. More detailed studies of the migrations, abundance, and wintering areas of whitefish species on the North Slope are required to ensure proper management. The Colville commercial fishery has been taking between 40,000 and 80,000 whitefish annually for the past 14 years. Further research is needed to determine if the fishery is now operating at maximum sustained harvest.

The importance of the Colville River delta areas and all other delta areas on the North Slope as rearing areas for young whitefish and other species should be considered before streambed alterations and gravel removal operations are carried out.

Acknowledgments — This investigation was conducted with U.S. Federal Aid in Fish Restoration funds.

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Occurrence of Hybrids Between Longnose Sucker (*Catostomus catostomus*) and White Sucker (*C. commersoni*) in Upper Kananaskis Reservoir, Alberta

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NELSON, J. S. 1973. Occurrence of hybrids between longnose sucker (*Catostomus catostomus*) and white sucker (*C. commersoni*) in Upper Kananaskis Reservoir, Alberta. J. Fish. Res. Board Can. 30: 557–560.

Hybrids between longnose sucker (*Catostomus catostomus*) and white sucker (*C. commersoni*), identified on the basis of intermediacy in several scale counts and in morphometric data, are recorded for the first time from Canada. The weakening of isolating mechanisms permitting hybridization was attributed to environmental factors, particularly species introduction and habitat disturbance. There was no evidence of swamping.

NELSON, J. S. 1973. Occurrence of hybrids between longnose sucker (*Catostomus catostomus*) and white sucker (*C. commersoni*) in Upper Kananaskis Reservoir, Alberta. J. Fish. Res. Board Can. 30: 557–560.

L'auteur signale pour la première fois au Canada des hybrides entre *Catostomus catostomus* et *C. commersoni*, identifiés par les valeurs intermédiaires de plusieurs comptages d'écailles et de caractères morphométriques. L'affaiblissement des mécanismes d'isolement permettant l'hybridation est attribuable à des facteurs de l'environnement, particulièrement l'introduction d'espèces et le dérangement de l'habitat. Il n'y a pas de signe de dominance.

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THE occurrence of hybrids of various species in the sucker family, Catostomidae, has been firmly established by Hubbs et al. (1943). Though hybridization is common between some of the species (Nelson 1968; Smith 1966; Schwartz 1972), longnose sucker (*Catostomus catostomus* (Forster)) and white sucker (*C. commersoni* (Lacépède)) apparently rarely hybridize although they occur together across much of northern North America. Hubbs et al. (1943) report five hybrids from the Platte River system in Colorado, Wyoming, and Nebraska. Brown (1971) notes hybridization between these two species from Montana. One hybrid (and the only one found to be still available) is a 312-mm standard length (SL) specimen collected in 1948 from the Missouri River and deposited in the University of Michigan Museum of Zoology (R. M. Bailey personal communication).

Hybrids of *C. catostomus* and *C. commersoni* from Canada are described in this report for the first time. They are from Upper Kananaskis Reservoir (50° 37′N, 115° 08′W), approximately 90 km southwest of Calgary at an elevation of about 1702 m, also the site of hybridization between lake chub (*Couesius plumbeus*) and longnose dace (*Rhinichthys cataractae*) (Nelson 1966, 1973).

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Materials and methods — Numerous young suckers, including some hybrids, were collected in 1968 by the author, in 1969 by N. Panter and B. Smiley, and in 1971 by N. Panter. In addition, 186- and 295-mm SL subadult hybrids were gillnetted August 14, 1969, and August 25, 1971, respectively.

Counts and measurements follow the definitions of Hubbs and Lagler (1964) except that head length (HL) excludes the opercular membrane. Several other characters, not described in Hubbs and Lagler (1964), are quantified as follows. The anterior scale count is made along the lateral line and terminates on the scale beneath the diagonal row employed in counting scales above the lateral line. Suborbital depth is the least distance from the orbit to the median plane on the lower surface; lip width, the greatest transverse distance across the lips; and lower lip length, the median distance from the mouth opening to the posterior midline junction of the lower lips when lightly held together (it is the least objective measurement). All measurements were made with dial calipers calibrated and read to the nearest 0.1 mm.

The criterion in identifying hybrids was general intermediacy between the two species in several characters within an individual. An examination of specimens of the two species from much of Alberta, in both allopatric and sympatric situations, failed to reveal morphological intermediates (the total number examined was much less than that examined from Upper Kananaskis Reservoir).

All hybrids collected are deposited in the University of Alberta Museum of Zoology (UAMZ). The two large hybrids are catalogued as UAMZ 3145 and 2743. The nine small hybrids shown in Fig. 2 are UAMZ 2841. Four additional small hybrids are UAMZ 2533.

Subadults — Two 186- and 295-mm SL individuals were recognized as hybrids by the general intermediacy of their scale counts (Table 1), of their head shape (Fig. 1), and of some other characters.

In scale counts, intermediacy occurred for anterior scales, scales above the lateral line, and caudal peduncle scales. The number of lateral line scales was similar to that for *C. commersoni* (and fell well within the total range known for this species). Paetz and Nelson (1970) give the following scale counts for the two species (only the last two columns are restricted to counts from Alberta material):

	Lateral line scales	Scales above lateral line	Caudal peduncle scales
C. catostomus	91–115	16–21	25–29
C. commersoni	55–85 (usually 58–68)	9–11	16–20

It is apparent that the hybrid specimens are unique only in the number of scales above the lateral line.

Dorsal fin rays overlap to a considerable extent between the two species. The relative placement of the two hybrids compared with 905 young of the parental species from Upper Kananaskis Reservoir was as follows:

No. rays	9	10	11	12	Total
C. catostomus	13	497	72	–	582
Hybrids		2	–	–	2
C. commersoni		23	251	49	323

For perfect intermediacy it would be necessary for one of the two hybrids to have 10 rays and the other 11. It is therefore not surprising that both of them happen to have 10. Interestingly, in *C. commersoni* counts of 11 much exceed counts of 12 for all Kananaskis material and limited material examined from elsewhere in Alberta, whereas in British Columbia the two counts occur with similar frequency (11's tending to be more than 12's, however) and with more 13's than 10's. High counts have also been reported in the east (e.g. Hubbs 1941, for New Hampshire) and Bailey and Allum (1962) found modes of 12 and 11 in eastern and western South Dakota, respectively.

Many differences exist between the parental species in head shape and mouth position. *C. catostomus* has a flattish dorsal profile and inferior mouth while *C. commersoni* has a convex profile and a subterminal mouth. Hybrids appear intermediate (Fig. 1). Specimens examined between 18 and 26 cm show that in the Upper Kananaskis Reservoir *C. commersoni* tend to have a greater head length and suborbital depth than *C. catostomus* but a lesser lower lip length and lip width. Although there is overlap in each trait, the ratio of head length to lower lip length plotted against suborbital depth to lip width showed the two hybrids falling clearly in an intermediate position (Fig. 2).

The two specimens also tend to be intermediate between *C. catostomus* and *C. commersoni* in head pigmentation differences (Fig. 1). Most noticeably, in *C. catostomus* there is a definite unpigmented band on the lower surface of the head that extends around the lower snout, in front of the mouth. In *C. commersoni* the snout in front of the mouth is broadly pigmented, the white band ending adjacent to the mouth and not as sharply set off from the dark upper parts as in *C. catostomus*. The largest hybrid has a continuous, narrow white band in

TABLE 1. Scale counts of 10 longnose sucker (*Catostomus catostomus*) and 10 white sucker (*C. commersoni*) selected at random from the Kananaskis system, and of each of the two subadult hybrids.

	Anterior scales		Lateral line scales		Scales above lateral line		Caudal peduncle scales
	Left	Right	Left	Right	Left	Right	
C. catostomus	52.6(49–59)[a]	50.9(46–56)	98.8(91–108)	98.8(91–109)	17.5(15–20)	17.8(15–20)	27.9(26–30)
Hybrids	37	39	65	63	12	14	25
	37	36	70	69	14	14	24
Mean of parental species	41.1	40.7	79.2	79.3	13.9	13.9	23.4
C. commersoni	29.7(28–32)	30.6(29–32)	59.6(57–62)	59.8(57–63)	10.3(9–11)	10.0(9–11)	19.0(17–20)

[a]Mean and range.

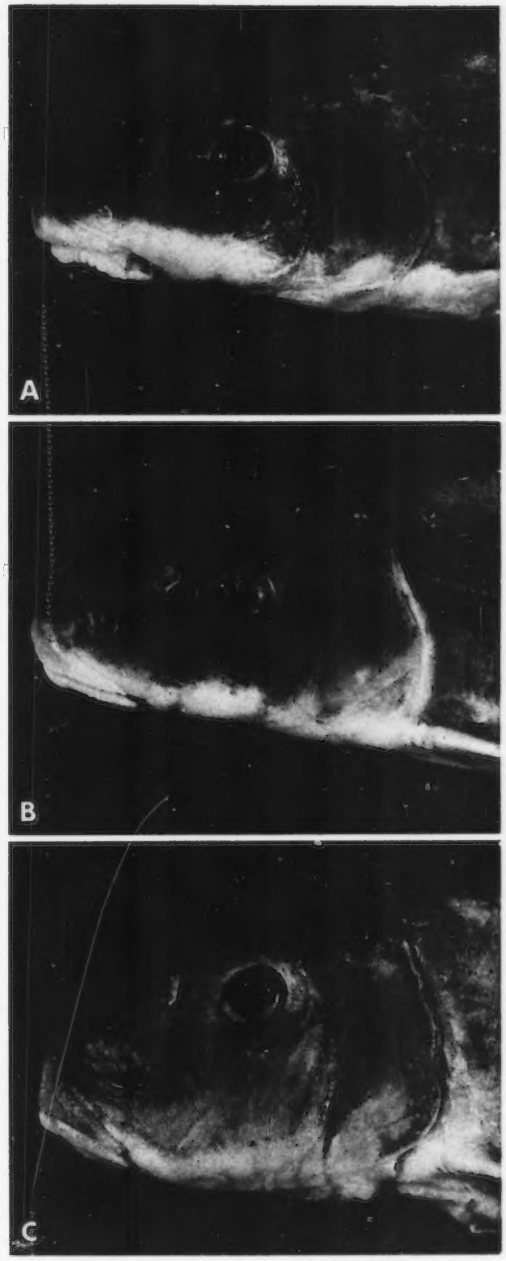

FIG. 1. A, *Catostomus catostomus* from Upper Kananaskis Reservoir, gillnetted August 14, 1969, of 289-mm SL and 44.4-mm HL; B, hybrid from Upper Kananaskis Reservoir, gillnetted August 14, 1969, of 284-mm SL and 47.5-mm HL; C, *C. commersoni* from Upper Kananaskis Reservoir, gillnetted August 14, 1969, of 290-mm SL and 49.1-mm HL.

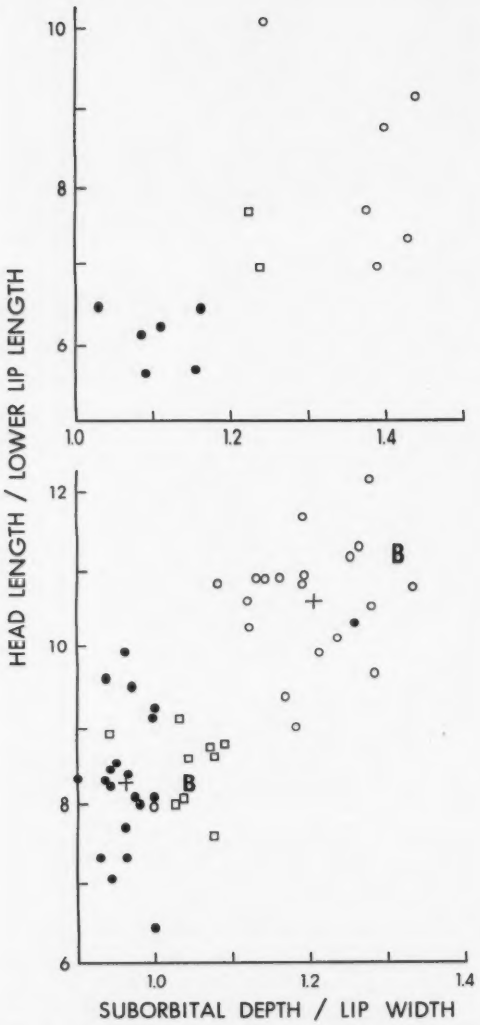

FIG. 2. Morphometric data used to infer presence of hybrids among large (top) and young (bottom) suckers (50–91-mm SL) from Upper Kananaskis Reservoir.

Top: Open circles, *C. commersoni*; solid circles, *C. catostomus*; and squares, hybrids.

Bottom: Open circles, specimens with 11 or more dorsal fin rays; solid circles, specimens with 10 or fewer. The 20 specimens in the upper right are *C. commersoni* and the 20 in the lower left *C. catostomus*. The nine squares represent specimens with "large" scales and taken to be hybrids; all have 10 or fewer dorsal rays. +'s, means for each of the parental samples; B's, means for 20 *C. catostomus* and eight *C. commersoni* from Barrier Reservoir, another reservoir in the Kananaskis system.

front of the upper lip while it is almost continuous in the 186-mm individual. In these individuals and in all young hybrids the triangular area adjacent to the posterior lip is usually pigment-free, as in *C. catostomus*. Although this and other color differences do not completely distinguish between hybrids and the parental species, they do at least agree with the other evidence.

Both sexes are represented in the large hybrids. The 186-mm specimen is a male while the 295-mm specimen is a female with immature eggs throughout the gonad. The female is shorter than the length at which maturity was first found in the Kananaskis system, at least for *C. commersoni*, in an earlier study (Nelson 1965).

Young — Young hybrids could not be diagnosed as accurately as the adults. However, there is little doubt that many specimens obtained in 3 years of collecting are hybrids. Accurate scale counts could not be made on many of these 50–91-mm SL specimens but they could be classified as either small scaled (typical *C. catostomus*) or large scaled (typical *C. commersoni*). Since the subadult hybrids were similar in lateral line scale count to *C. commersoni*, young hybrids would be expected to appear large scaled, like *C. commersoni*. The morphometric analysis found useful in separating adults, when used on young specimens, produced a good separation and nine out of several more fish picked out as looking intermediate (e.g. with crowded anterior scales) had large scales like those of *C. commersoni* but had head proportions like those of *C. catostomus*, although more *C. commersoni-like* than typical *C. catostomus* (Fig. 2). Better discrimination could be attained by correcting for allometric growth.

Of the nine hybrids, one specimen had eight dorsal fin rays, two had nine rays, and six had ten rays. Four additional specimens (55–63-mm SL), also considered to be hybrids, all had 11 dorsal rays. Color differences, although somewhat different from those for adults, showed that young hybrids were intermediate between the parental species.

Discussion — The intermediacy in several characters in two subadult and 13 young specimens makes it almost certain that most or all of these morphological intermediates are of hybrid origin. The hybrids, in general, agree with the hybrids of the same parental cross described in the extensive study of Hubbs et al. (1943).

Some of the environmental factors thought to weaken isolating mechanisms and permit hybridization are present in this study. Both species, though native to the Bow River, are introductions to the Upper Kananaskis Reservoir and the environment is a disturbed one, with marked fluctuations in water level due to hydroelectric development (Nelson 1965). Introduction has been noted to be associated with hybridization in *C. commersoni* elsewhere. Baxter and Simon (1970) report hybridization of *C. commersoni* with *C. latipinnis* and with *C. discobolus* in an area where *C. commersoni* has apparently been introduced. However, hybridization between *C. commersoni* and *C. macrocheilus* appears to be occurring in natural conditions (Nelson 1968). Young and adult *C. catostomus* were collected in much greater numbers than *C. commersoni* from Upper Kananaskis Reservoir in 1961 (Nelson 1965). Disproportionate numbers were also found in this study, again with *C. catostomus* the predominant sucker, but this need not be a causal factor of hybridization in this case.

In many strictly sympatric situations temporal isolation probably limits the opportunity for hybridization but would not prevent it. *Catostomus catostomus* peaks in spawning time before *C. commersoni* in British Columbia (Geen et al. 1966; personal observations) and in some creeks there appears to be little overlap in spawning time (e.g. Cluculz drainage). In the Kananaskis system the two species spawn at about the same time in Barrier Reservoir and, probably, in Upper Kananaskis Reservoir.

Present evidence does not suggest that hybridization is breaking down the integrity of the parental species (i.e. there is no evidence of swamping) in Upper Kananaskis Reservoir. A comparison of the two suckers in areas outside Upper Kananaskis Reservoir left no reason for believing that introgression is occurring.

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Influence of Lead and other Metals on Fish δ-Aminolevulinate Dehydrase Activity[1]

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JACKIM, E., 1973. Influence of lead and other metals on fish δ-aminolevulinate dehydrase activity. J. Fish. Res. Board Can. 30: 560–562.

Exposing mummichog (*Fundulus heteroclitus*) and winter flounder (*Pseudopleuronectes americanus*) to sublethal concentrations of lead resulted in reduction of liver and kidney δ-aminolevulinic acid dehydrase activity. The results of this project are expected to afford an index of response to heavy metals in estuarine waters.

JACKIM, E., 1973. Influence of lead and other metals on fish δ-aminolevulinate dehydrase activity. J. Fish. Res. Board Can. 30: 560–562.

L'exposition de choquemorts (*Fundulus heteroclitus*) et de plies rouges (*Pseudopleuronectes americanus*) à des concentrations sublétales de plomb cause une diminution d'activité de la cette δ-aminolévulinate acide déshydrogénase du foie et du rein. On s'attend que les résultats de étude fournisse un indice de réponse aux hautes concentrations de métaux dans les estuaires.

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IT has been shown previously that δ-aminolevulinic acid dehydrase (ALA-D) activity is inhibited by lead in human erythrocytes (Bonsignore et al. 1965) and ox liver and kidney preparations (Gibson et al. 1955). Recent reports demonstrated this enzyme to be a valuable diagnostic indicator of lead poisoning and even chronic exposure to lead in people (Hernberg and Nikkanen 1970).

Because of the reported sensitivity of this enzyme to lead, the present study was initiated to determine whether ALA-D could be used in evaluating lead exposure and sublethal toxicity in fish. Specificity of inhibition was determined by measuring activity of ALA-D following exposures of fishes to other common heavy metal salts. Mummichog (*Fundulus heteroclitus*) and winter flounder (*Pseudopleuronectes americanus*) were used in these studies.

Present procedure followed earlier studies on fish liver enzymes (Jackim et al. 1970).

Materials and methods — Mummichogs and small flounder caught near Point Judith, R. I., were acclimated at 20 C for a minimum of 2 weeks prior to exposures.

[1]Contribution No. 45 from the National Marine Water Quality Laboratory. This work was conducted as part of EPA Project 16 AAT in support of the development of water quality criteria for the protection of marine aquatic life and wildlife.

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Mummichogs were exposed in 20-liter jars containing 16 liters of unfiltered sea water. Six fish of undetermined sex weighing 3–5.5 g were placed in each jar 2 hr after addition of each metal salt. Jars were continually aerated and filtered with fiberglass aquarium filters. Flounder weighing 20–40 g were treated similarly except that only two fish were placed in each jar. Fish were not fed during the first 96 hr. Thereafter they were fed ground clam tissue daily. During these studies fish were exposed to a photoperiod approximating normal day–night cycle.

Metal salts were added in sublethal concentrations (shown in results section). None of the fish died or appeared moribund during exposures. Metal chlorides were used in all cases except for lead and silver, which were added as nitrates. Water samples were withdrawn periodically for residual metal analysis by anodic stripping, atomic absorption spectroscopy, and flameless atomic absorption for mercury.

Fish were removed from their containers after exposure and rinsed with cold distilled water to remove external metal contamination. Fish were then decapitated and livers removed. Three *Fundulus* livers were pooled for each assay. Organs were weighed and homogenized as a 1:10 w/v dilution with cold 0.15-M KCl solution by 10 passes through a power-driven tissue grinder. Flounder were treated identically except that livers were assayed individually.

ALA-D activity was determined by a procedure based on the method of Bonsignore et al. (1965). One half milliliter of the crude liver homogenate was added to 0.5 ml of 0.1-M phosphate buffer, *p*H 6.8. The reaction was started by addition of 0.5 ml of freshly prepared 0.01-M δ-aminolevulinic acid solution adjusted to *p*H 7 with sodium bicarbonate. The preparation was quickly mixed, 0.5 ml withdrawn for a zero time blank, and the remainder was placed in a 35 C incubation bath for exactly 1 hr. The reaction was stopped by introducing 0.5-ml aliquots of reaction mixture into 10-ml centrifuge tubes containing 0.5 ml of 0.1-M $HgCl_2$ in 10% trichloroacetic acid, followed by mixing on a vortex mixer. The mixture is centrifuged at 2000 rpm for 10 min in a clinical centrifuge and 0.5 ml of clear supernatent withdrawn for porphobilinogen determination. This reaction product is assayed by mixing with equal portions of Ehrlichs reagent, which is made by dissolving 1-g dimethylaminobenzaldhyde in 20-ml acetic acid and adding 16-ml 70% perchloric acid, and brought to a volume of 50 ml with glacial acetic acid (Marizerall and Granick 1956). The color reagent and sample are allowed to react for 5 min, and the optical density is read against distilled water at 555 nm in a DB-G spectrophotometer.

Protein content of the remaining reaction mixture was assayed by the Lowry method modified for use with a Technicon Autoanalyzer (Bartley and Polidik 1967).

Enzyme activity was expressed as the change in optical density during a 1-hr incubation divided by the protein concentration (grams per milliliter) of the reaction mixture. The percentage change in enzyme activity with respect to controls is also used because the absolute values are not entirely consistent from one experiment to the next. Significance of difference between groups was determined by the Fisher "*t*" test.

Results — Mummichogs exposed to an initia concentration of 10 ppm lead (as nitrate) for 2 weeks showed no apparent ill effects or abnormal behavioral changes. ALA-D activity of the lead nitrate treated fish decreased by 22% after a 96-hr exposure and 18.5% at the end of the 2 weeks. Difference between the means of control and exposed animals was significant to 0.05 and 0.01 levels of confidence, respectively.

An evaluation of variability in unexposed control killifish in 10 experiments conducted over a 4-month period produced a mean enzyme activity of 19.9-units/g protein with a range between 16 and 24 and a standard deviation of 2.6.

An experiment using *Fundulus*, designed to compare effects of 50 ppm lead and 0.02 ppm mercury (initial concentrations) over a prolonged time, demonstrated that both metals produced a marked inhibition of ALA-D in the early stages with a subsequent partial recovery in the mercury-treated fish (Fig. 1). The behavior of lead nitrate treated fish was unaffected throughout the experiment. Mercury-exposed fish were noticeably more excitable but otherwise appeared the same as the control fish.

To determine the specificity of ALA-D inhibition, *Fundulus* were exposed to sublethal concentrations (Table 1) of various toxic metal salts for 4 and 14 days. Table 1 shows that lead produces the greatest decrease in activity while other metals, namely cadmium, zinc, and silver, increased ALA-D activity.

Lead produced an average 66% decrease in ALA-D activity in three flounder livers when animals

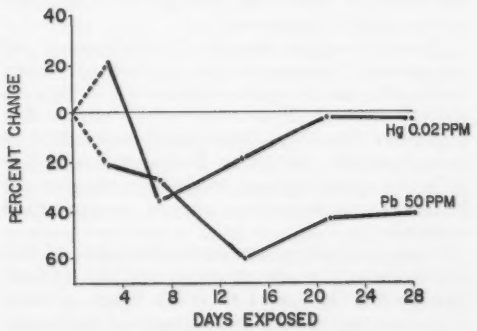

FIG. 1. ALA-D inhibition and activation vs. time for mummichog (*Fundulus heteroclitus*) exposed to mercury and lead salts. Each point represents a value produced by three pooled livers as compared to that from three pooled control animals assayed simultaneously. The initial concentration was 50 ppm for lead and 0.02 ppm for mercury. The final concentration of lead and mercury was 1 and 0.012 ppm, respectively.

TABLE 1. Effects of exposure to various metals on mummichog. (*Fundulus heteroclitus*) liver ALA-D. Activity is expressed as change in optical density per hour per gram protein. The figures are from a typical experiment in which each value is obtained from pooled livers of three fish.

Initial concn (*ppm*)	Metal	96 hr		2 weeks		Final concn (*ppm*)
		Activity	% change	Activity	% change	
–	control	18	–	14	–	–
1	Cu^{++}	16	−11.7	13	−7	0.6
10	Cd^{++}	20	+10	15	+7	10
10	Pb^{++}	14	−22	11	−19	0.8
10	Zn^{++}	18	0	18	+29	2.2
0.02	Ag^{+}	26	+45.6	16	+14	<.02

were exposed for 1 week to a 10 ppm initial concentration. Kidney tissues from the same animals exhibited a 58% decrease in ALA-D activity with respect to controls.

Discussion — Lead decreased ALA-D activity in both acute and chronic exposures in fish, as expected on the basis of reported mammalian studies. Even though this inhibition is not unique to lead, it appears to be limited to a few toxic heavy metals, namely lead, mercury, and copper.

ALA-D is believed to possess essential thiol groups that are subject to inactivation by heavy metals (Gibson et al. 1955). As with other enzymes (Jackim et al. 1970), some heavy metals increase enzyme activity at least during early periods of exposure or at lower concentrations. Zinc, silver, and, to a lesser extent, cadmium acted in this manner (Table 1). Induction of some liver enzymes is a common toxicological phenomenon.

The results suggest that ALA-D depression is one characteristic response to lead exposure or toxicity in fish although it is by no means a specific response to such stress. In all instances it is understood that unexposed fish of the same species should serve as controls in such evaluations. It appears that ALA-D values in control fish are rather consistent and not influenced markedly by common environmental variability.

It was reported previously that lead also inhibits ribonuclease, acid phosphatase, xanthine oxidase, and catalase (Jackim et al. 1970). Which of these enzymes is actually the best indicator of lead pollution effects on fish remains to be determined under various environmental conditions.

In this and other studies involving heavy metals in closed marine systems, the problem of toxicant solubility makes it difficult to relate enzyme activity to pollutant concentrations other than by considering that the organisms are exposed to decreasing levels of toxicant. It is also important to note that pollutants will come out of solution at varying rates, and this, in itself, is an important variable to consider in evaluating toxicity. For instance, a 50 ppm addition of lead decreased to 0.7 ppm total lead in 24 hr and remained at this level indefinitely.

Also, mercury drops from an initial concentration of 0.22 ppm to about 0.01 ppm in the tank and remains at that level up to 1 week. The question consequently arises, "Is the decreased effect on enzyme activity upon prolonged treatment (as seen in Table 1) due to some kind of an adaptation of the animal, or is it simply resulting from a decrease in available toxicant?" Further work is needed to answer this question adequately.

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Occurrence of the Shortnose Sturgeon (*Acipenser brevirostrum*), an Endangered Species, in Montsweag Bay, Maine

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FRIED, S. M., AND J. D. MCCLEAVE. 1973. Occurrence of the shortnose sturgeon (*Acipenser brevirostrum*), an endangered species, in Montsweag Bay, Maine. J. Fish. Res. Board Can. 30: 563–564.

Thirty-one shortnose sturgeon (*Acipenser brevirostrum*) were caught in gillnets in Montsweag Bay in the Sheepscot River system during June and July of 1971 and 1972. Of nine fish preserved for study, six were longer than any previously documented and four exceeded the maximum total length previously postulated. These specimens represent the second population of this endangered species found in the Gulf of Maine.

FRIED, S. M., AND J. D. MCCLEAVE. 1973. Occurrence of the shortnose sturgeon (*Acipenser brevirostrum*), an endangered species, in Montsweag Bay, Maine. J. Fish. Res. Board Can. 30: 563–564.

Trente-et-un esturgeons à museau court (*Acipenser brevirostrum*) ont été capturés dans des filets maillants dans la baie Montsweag, dans le système de la rivière Sheepscot, en juin et juillet 1971 et 1972. Parmi les neuf poissons conservés pour étude, six dépassaient tous les records de longueur publiés à date, et quatre excédaient le maximum de longueur totale considéré comme admis à venir jusqu'ici. Ces individus représentent la deuxième population de cette espèce, dont la survie est en danger, à se trouver dans le golfe du Maine.

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DURING the summers of 1971 and 1972, 31 sturgeon were captured in gillnets on mudflats in Montsweag Bay in the Sheepscot River system (U.S.C.G.S. chart 314). A single specimen was also caught in the upper Sheepscot River estuary. Nine fish were preserved and identified as shortnose sturgeon (*Acipenser brevirostrum*). The others were tentatively identified as shortnose sturgeon and released.

Although a population of this species exists as far north as the Saint John River, N. B. (Leim and Day 1959; Leim and Scott 1966; W. B. Scott personal communication), only one other documentation (Bigelow and Schroeder 1953) exists for the Gulf of Maine, for a single specimen captured off Provincetown, Mass.

The shortnose sturgeon is a rare and endangered species (Anon. 1970; McAllister 1970; Miller 1972), yet it is fairly common in Montsweag Bay. Also, four of the preserved specimens exceed the previously reported maximum total length of 100 cm (Bigelow and Schroeder 1953; Vladykov and Greeley 1963).

Fish were initially preserved in 10% formalin and later transferred to 50% propanol. Specimens were identified with a key to the Acipenseroidei of the Western North Atlantic (Vladykov and Greeley 1963).

All sturgeon examined had the blackish viscera distinctive of the species (Bean 1903; Bigelow and Schroeder 1953; Vladykov and Greeley 1963). The preanal and postdorsal shields were weakly developed in all nine fish. Count and measurement averages closely agreed with those given by Vladykov and Greeley (1963) (Table 1). However, in two fish the difference between total length and fork length was greater than 12% of the fork length; in two others the interorbital width as a percentage of head length was below the previous range; in four specimens the mouth width as a percentage of interorbital width was below the previous range; and in three the lateral shield count was below the previous range. Six of the specimens were longer than any previously recorded (Koski et al. 1971; Vladykov and Greeley 1963) and four exceeded the maximum total length previously postulated (100 cm) (Bigelow and Schroeder 1953; Vladykov and Greeley 1963). All but the two smallest sturgeon were females, some containing eggs approximately 1.5 mm in diameter.

Since sampling was done only during June and July of 1971 and 1972, it is not known if the short-

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TABLE 1. Morphometric ratios (× 100) and counts for nine shortnose sturgeon (*Acipenser brevirostrum*) from Montsweag Bay and comparisons with data from Vladykov and Greeley (1963). (TL = total length; FL = fork length; HL = head length; SL = snout length; POD = postorbital distance; IOW = interorbital width; MW = mouth width).

Total length (*cm*)	TL–FL	HL	SL	POD	IOW	MW	No. gillrakers (*first arch*)	No. shields		
	FL	FL	POD	HL	HL	IOW		Dorsal	Lateral	Ventral
80.7	12	19	89	53	39	69	25	9	28	7
87.9	14	22	78	55	34	72	22	10	28	9
92.0	11	20	73	55	32	64	22	10	24	8
94.6	10	20	67	59	39	66	29	11	29	9
96.5	9	21	64	62	34	67	27	9	29	9
102.9	6	21	67	57	31	70	26	11	24	9
103.4	9	20	81	53	38	66	27	9	29	9
104.3	14	18	80	58	40	74	29	10	27	8
118.1	10	20	64	58	36	69	29	9	24	8
Avg.	10.6	19.9	73	56.7	35.9	68.6	26.2	9.8	26.9	8.4
Avg. and range (Vladykov and Greeley 1963)	11	22	70	55	37	74	25.5	10	28	8
	–	–	–	(51–61)	(34–40)	(69–81)	(22–29)	(8–13)	(25–32)	(7–10)

nose sturgeon is present in the Sheepscot system throughout the year. Little is known of the migration of the shortnose sturgeon. It is possible that the Montsweag Bay individuals belong to populations from elsewhere in the Gulf of Maine or nearby rivers such as the Kennebec River.

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Parasitism on Juvenile Pacific Salmon (*Oncorhynchus*) and Pacific Herring (*Clupea harengus pallasi*) in the Strait of Georgia by the River Lamprey (*Lampetra ayresi*)

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Roos, J. F., P. Gilhousen, S. R. Killick, and E. R. Zyblut. 1973. Parasitism on juvenile Pacific salmon (*Oncorhynchus*) and Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia by the river lamprey (*Lampetra ayresi*). J. Fish. Res. Board Can. 30: 565–568.

River lamprey (*Lampetra ayresi*) were found to parasitize the young of five species of Pacific salmon (*Oncorhynchus*) and Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia, B.C. The dorsal attachment of the river lamprey is in sharp contrast to the usually ventral attachment of other species of lampreys that parasitize salmonids. Up to 1.9% of young salmon showed evidence of lamprey marks, and marked fish were generally restricted to a narrow size-range. Some of the fish exhibited severe wounds. Evidence from healing wounds on fingerlings and scars on adults indicates that some juvenile salmon survive the attacks of the river lamprey.

Roos, J. F., P. Gilhousen, S. R. Killick, and E. R. Zyblut. 1973. Parasitism on juvenile Pacific salmon (*Oncorhynchus*) and Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia by the river lamprey (*Lampetra ayresi*). J. Fish. Res. Board Can. 30: 565–568.

Nous avons observé des lamproies à queue noire (*Lampetra ayresi*) sur les jeunes de cinq espèces de saumons (*Oncorhynchus*) et sur le hareng du Pacifique (*Clupea harengus pallasi*), dans le détroit de Georgie, C.-B. La fixation dorsale de la lamproie à queue noire forme un contraste frappant avec la fixation ordinairement ventrale des autres espèces de lamproies parasites des salmonidés. Jusqu'à 1.9% des saumonneaux portent des marques de lamproies, et les poissons parasités sont généralement compris dans une gamme restreinte de longueurs. Certains poissons portent des blessures sérieuses. Les blessures en voie de guérison chez les alevins et les cicatrices chez les adultes démontrent que quelques saumonneaux survivent aux attaques de la lamproie à queue noire.

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Parasitism of adult Pacific salmon (*Oncorhynchus*) by the Pacific lamprey (*Entosphenus tridentatus*) has been observed frequently (Birman 1950; Williams and Gilhousen 1968) but parasitism of juvenile salmon by the river lamprey (*Lampetra ayresi*) in Pacific coast waters has not been documented extensively (Clemens and Wilby 1961).

Little is known about the life history of the river lamprey. Distribution of this species, as reported by Carl et al. (1959), is from San Francisco Bay north to the Skeena River. Carl et al. (1959) report that specimens of *L. ayresi* have been taken attached to herring strips trolled by sport fishermen; however, they concluded that *L. ayresi* is probably uncommon in British Columbia waters. Pletcher (1963) reported that *L. ayresi* is parasitic and is common to Strait of Georgia waters during the summer months. Vladykov and Follett (1958) reported that kokanee (*O. nerka*) in Lake Washington, Seattle, Wash., had been parasitized by *L. ayresi*. Miller et al. (1968) reported that predation by *L. ayresi* was observed on numerous occasions in the Duwamish Estuary at Seattle, Wash., "Many specimens of chinook salmon taken in the estuary bore either fresh lamprey wounds or scars and several were taken with lampreys firmly attached to the dorsolateral surface." Whithler (1955) noted that a young coho salmon (*O. kisutch*) 92 mm long was picked up in the Skeena River,

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B.C., on July 16, 1955, with a 162-mm lamprey (*L. ayresi*) firmly attached to the right side above the lateral line and above the anterior half of the anal fin. A deep flesh wound (5 × 3 × 2 mm deep) was caused by the lamprey.

In late May 1971, a bait herring fisherman at Bargain Harbour, B.C., reported seeing unusual numbers of small lampreys attached to Pacific herring (*Clupea harengus pallasi*). In addition, small salmon were seen bearing similar wounds, and in one instance a lamprey was noted attached to a juvenile salmon. Lampreys were later identified as *L. ayresi*. The present paper documents the nature and extent of *L. ayresi* parasitism in recent years in the Strait of Georgia inferred from wounds on juvenile salmon of five species, on adult sockeye, and on herring.

Materials and Methods — Samples of young sockeye and chinook salmon (*O. nerka* and *O. tshawytscha*, respectively), herring, and lampreys were obtained from Bargain Harbour (Fig. 1) between May 24 and June 14, 1971. Fish were captured in a bait herring purse seine 193.8 m long by 22.1 m deep, made of 2.5-cm mesh netting.

FIG. 1. Strait of Georgia area where juvenile salmon and adult herring were sampled.

Juvenile chinook salmon and coho salmon were captured off the mouth of the Fraser River (Fig. 1) with a purse seine from July 15 to August 29, 1970. The purse seine was 258.5 m long and 18.5 m deep and mesh netting varied from 0.6 to 5.1 cm. Fish captured were measured for length and inspected for lamprey marks.

Preserved samples of fingerling pink (*O. gorbuscha*) salmon taken during 1968–1970 in June, July, and August along the shores of the Gulf Islands and southern Vancouver Island were re-examined. Also, preserved chum salmon (*O. keta*) collected from April 13 to August 29, 1970, in the Strait of Georgia off the Big Qualicum River (Fig. 1) were examined for lamprey marks. These samples had been taken with purse seine, beach seine, or dipnet.

Adult Fraser River sockeye salmon from commercial catches in 1971 and 1972 were examined for scars that may have resulted from *L. ayresi* attacks earlier in their life cycle.

Juveniles — Bargain Harbour — A total of 33 young sockeye salmon were taken at Bargain Harbour. Fork length of the fish ranged from 86 to 172 mm. Sockeye that were marked (26) ranged in length from 88 to 110 mm. These samples were selected, therefore per cent of fish wounded was not representative. In addition to the young salmon, seven lampreys averaging 127 mm in length (range, 114–143 mm) were captured and identified as *L. ayresi* (Vladykov and Follett 1958).

Wounds on marked sockeye varied from one to three per fish. Most of the marks were on the dorsal surface anterior to the dorsal fin (Fig. 2) and none were on the head or tail or wholly below the lateral line. All marks examined showed considerable removal of flesh. Several fish had lesions up to 8 mm in diameter, which is about the size of the oral sucking disc of the river lampreys obtained at Bargain Harbour. Flesh penetration was from 1 to 3 mm and some sockeye bore linear wounds as long as 22 mm. In most attacks, skin was removed entirely from the area.

Wounds on Bargain Harbour herring (128–144 mm) were similar to those found on sockeye (Fig. 2). A lamprey was photographed attached to a herring in the bait herring net (Fig. 3) and the point of attachment was almost identical to the location of the wound on the herring shown in Fig. 2.

Juvenile chinook salmon had marks similar to those noticed on sockeye but there was evidence of healing (Fig. 4) in some fish. The upper fish in Fig. 4 shows a healing wound between the dorsal fin and the lateral line. The lower fish in Fig. 4 has a small healing wound below the dorsal fin in addition to a large open wound behind the head that exposed the neural spines.

Fraser River Mouth — A total of 1465 juvenile chinook salmon were taken off the mouth of the

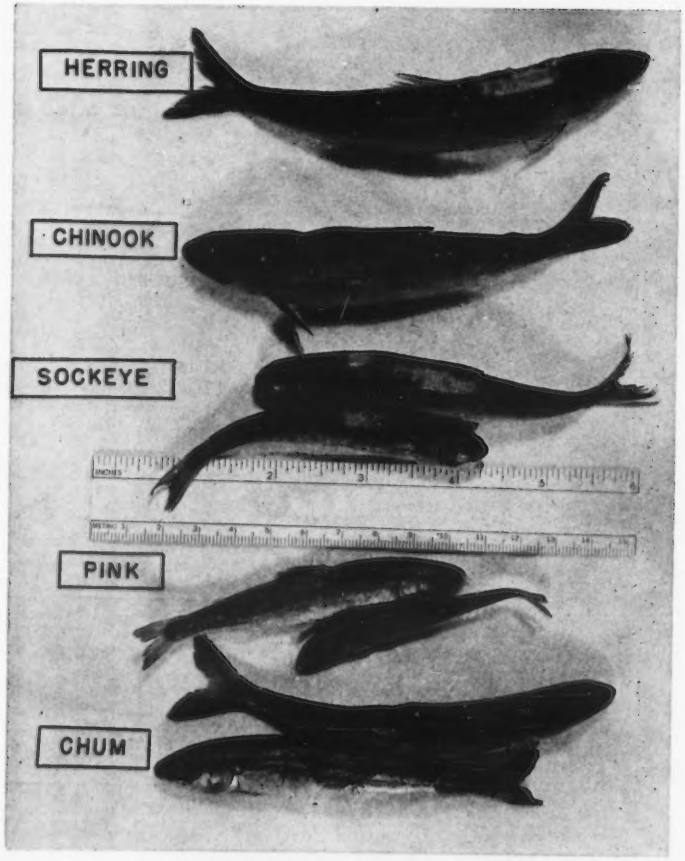

FIG. 2. Wounds on young salmon and herring.

FIG. 3. Lamprey attached to herring in purse seine.

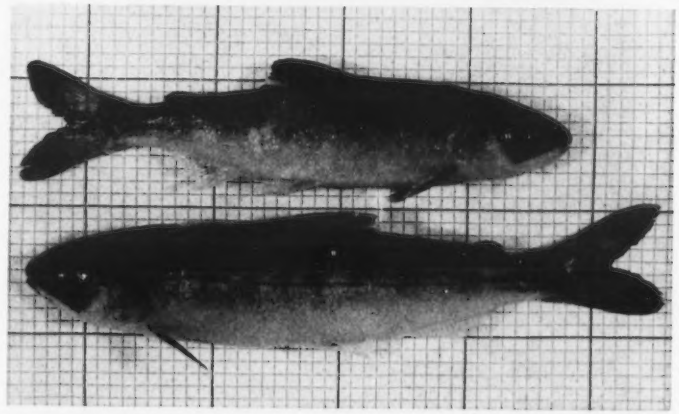

FIG. 4. Wounds on young chinook salmon. Background is 10 divisions to the inch.

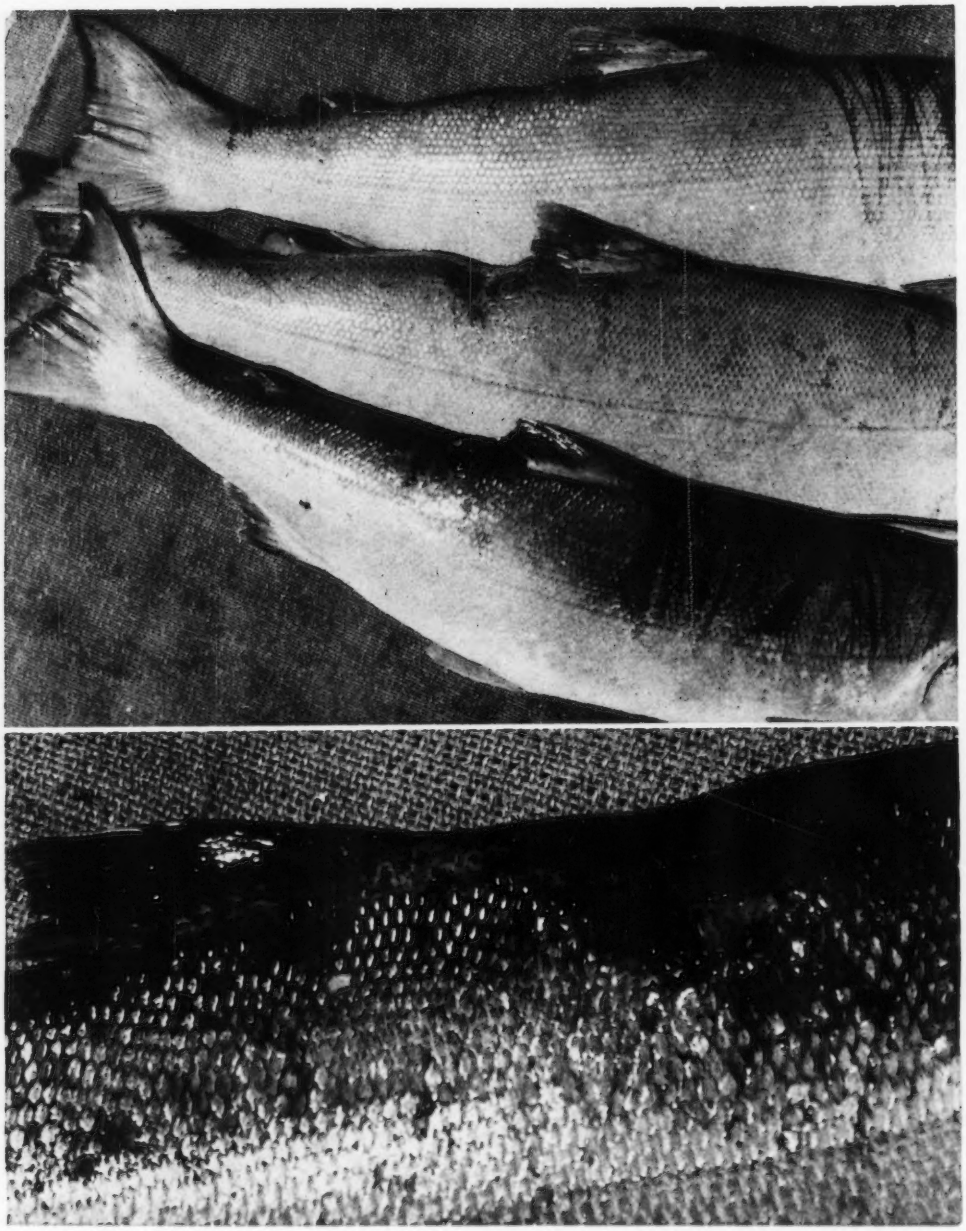

FIG. 5. Adult sockeye caught in the Fraser River in 1971 (*upper*) and in Juan de Fuca Strait in 1972 (*lower*) showing possible healed *L. ayresi* wounds.

Fraser River. Only 26 fish (1.8%) were found to have marks, all above the lateral line, suggesting attacks by *L. ayresi*. Fish with lamprey marks had a fork length range of 115–280 mm whereas the size of chinooks captured ranged from 75 to 525 mm.

A total of 214 juvenile coho salmon were captured with the chinook, and four (1.9%) had lamprey marks, about the same incidence as that determined for chinook. All marks were above the lateral line suggesting attacks by *L. ayresi*. The coho ranged in size from 88 to 610 mm; however, fish that were marked ranged only from 195 to 200 mm.

Gulf Islands — Wounds similar to those found on young salmon at Bargain Harbour and Fraser River mouth were occasionally noted on juvenile pink salmon (Fig. 2) netted along the Gulf Islands. In most catches, no marked pinks were found but, at specific locations, wounded pinks sometimes formed as much as 1% of the catch.

Big Qualicum River — A total of 2015 juvenile chum salmon were captured off the Big Qualicum River. Six fish (0.3%) were found to have lamprey marks located along the dorsal portion of the fish (Fig. 2), suggesting attacks by *L. ayresi*. Marked fish had a fork length range of 94–115 mm while the range in the entire sample was from 31 to 151 mm, (sample mean, 56.6 mm).

Adult Salmon — Adult sockeye returning to the Fraser River in 1971 were examined for wounds of various types (Gilhousen 1972). Of 1880 sockeye examined, approximately 1.5% had healed dorsal–dorsolateral wounds (Fig. 5) possibly attributable to *L. ayresi* attacks. Sockeye in 1972 were also examined (1858 fish) and several fish (0.9%) bearing possible healed *L. ayresi* marks were observed (Fig. 5).

Discussion — This study revealed that the young of five species of Pacific salmon are subject to predatory attacks by *L. ayresi* in the Strait of Georgia area.

All marks observed on young salmon in the present study were on the dorsal or dorsolateral surface of the fish. Previous published reports also indicated that *L. ayresi* attacks were confined exclusively to the dorsal area. This is in contrast to the mainly ventral attacks by *Entosphenus* and *Petromyzon*. Williams and Gilhousen (1968) reported that about 80% of the attacks by *Entosphenus* were on the ventral areas of adult sockeye salmon while Davis (1967), in studies on landlocked Atlantic salmon (*Salmo salar*), determined that 83% of marks by *Petromyzon* were noted on the ventral surface. Lennon (1954) and Wigley (1959) also reported that most marks by the sea lamprey were below the lateral line.

The highest incidence of marked fish was about 2% which suggests that *L. ayresi* predation is presently limited to a small proportion of the young salmon utilizing the Strait of Georgia area. On the other hand, studies on larger salmonids have indicated a much higher incidence of predation by other species of lamprey. Williams and Gilhousen (1968) noted that 67% of adult sockeye salmon were marked by the Pacific lamprey. In addition, Davis (1967) reported that 85% of all salmon examined had been attacked by the sea lamprey (*Petromyzon marinus*), and some fish had as many as eight separate wounds.

Lampetra ayresi in the Strait of Georgia appeared to attack only intermediate sized chinook, coho, and chum salmon. Size selectivity was also noted by Davis (1967), who reported that the sea lamprey attacked larger salmon more frequently than smaller fish. Parker and Lennon (1956) also observed in aquarium studies of sea lampreys that small hosts showed fewer marks than large ones.

Although the occurrence of healing wounds on young salmon, and of scars on adults, indicated some parasitized juveniles survived to be adults, the depth and length of some of the wounds observed in the present study could possibly result in premature death in salmon fingerlings and herring. The evidence obtained from this limited study, however, does not provide sufficient information to estimate mortality attributable to *L. ayresi* predation.

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Effects of Temperature on Mortality of Fingerling Channel Catfish (*Ictalurus punctatus*) Experimentally Infected with Channel Catfish Virus

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When water temperature was reduced from 28 to 19 C for channel catfish (*Ictalurus punctatus*) fingerlings 24 hr after injection with channel catfish virus (CCV), 24% mortality occurred. In comparison, fish held at a constant temperature of 28 C had a mortality of 94% and those held in 19 C water had 14% mortality. Reducing the temperature to 19 C when the first deaths occurred at 28 C (64–72 hr after injection) resulted in 78% mortality. Insignificant mortality occurred in fish injected with Hanks' balanced salt solution. Results of temperature change are discussed as to their potential value in reducing the effects of CCV disease under cultural conditions.

PLUMB, J. A. 1973. Effects of temperature on mortality of fingerling channel catfish (*Ictalurus punctatus*) experimentally infected with channel catfish virus. J. Fish. Res. Board Can. 30: 568–570.

Des alevins de barbue (*Ictalurus punctatus*) soumis à un abaissement de température de 28 à 19 C, 24 heures après injection du virus de la barbue (CCV), subissent des mortalités de 24.3%. Par comparaison, les poissons maintenus dans une eau de température constante à 28 C ont un taux de mortalité de 94.2%, et à 19 C un taux de 14.1%. L'abaissement de la température au début des mortalités (64 à 72 heures après injection) entraîne des mortalités de 78.3%. Nous discutons des possibilités qu'offrent les changements de température visant à minimiser les effets de la maladie à virus de la barbue dans des conditions d'élevage.

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CHANNEL catfish virus disease (CCVD) has been diagnosed in catfish cultural operations throughout the southern United States during summer months (Fijan 1968; Plumb 1971), when susceptible fingerling fish are abundant and water temperatures above 25 C are commonplace in hatchery ponds. This report deals with effects of temperature on the percentage of mortality in fingerling channel catfish (*Ictalurus punctatus*) experimentally infected with CCV. The objective of the study was to determine if lowering the water temperature from 28 to 19 C at various times after injection with the virus would reduce the percentage of mortality in infected fish, and whether raising it to 28 C from 19 C would increase the mortality. Temperature manipulation to reduce the mortality rate of salmonids infected with infectious hematopoietic necrosis virus was reported by Amend (1970).

Materials and methods — Nine-month-old channel catfish fingerlings from the Fisheries Research Unit, Alabama Agricultural Experiment Station, Auburn, Alabama, were used in the study. The fish averaged 4.8 g and 8.9 cm total length.

The CCV isolate reported by Fijan (1968), later described by Fijan et al. (1970) and characterized by Wolf and Darlington (1971), was used for infection. This strain had been maintained for 4 years by repeated passage in brown bullhead (*Ictalurus nebulosis*) cell cultures (ATCC No. 59). Infection was produced by injecting each fish intraperitoneally with 0.1 ml of Hank's balanced salt solution (HBSS) containing 100–560 tissue culture infectious doses (50% endpoint). Virus titer was made in brown bullhead cultures grown in 16 × 125 mm tubes and the endpoint determined by the method of Reed and Muench (1938).

The tests were conducted in 40-liter aquaria filled with dechlorinated municipal water, each aquarium with 10 fish. In each of two trials, three aquaria were used for each temperature regime (Table 1). Temperature was raised to and kept at 28 C with heaters, and kept at or lowered to 19 C with a room air conditioner.

The virus-injected fish were placed initially in aquaria at 19 C. For the tests in which the temperature was reduced to 19 C from 28 C, the aquaria were warmed to 28 C immediately after the fish were introduced. The intervals at which the temperatures were reduced were: 24 hr after injection; when the first deaths occurred in 28 C aquaria (64–72 hr after injection); and 96 hr after injection.

For the tests in which the temperature was raised to 28 C from 19 C, the temperature changes were effected within 6–8 hr after the heaters were transferred from the aquaria used in the previous tests. During the transfers, the heaters were disinfected in 100 ppm chlorine (Fijan et al. 1970) and thoroughly rinsed.

All tests were terminated after 14 days due to the appearance of bacterial and fungal diseases in surviving fish.

TABLE 1. Percentage mortalities of channel catfish fingerlings (10 fish in each of 6 aquaria) 14 days after injection with channel catfish virus when temperature was held at 28 C and reduced to 19 C, and held at 19 C and raised to 28 C, at three intervals.

Temperature regime	Mean	Range
Constant 28 C	94	90–100
Reduced to 19 C		
24 hr after injection	24[a]	0–50
at first deaths[b]	78	50–100
96 hr after injection	68	40–100
Constant 19 C	14	0–30
Raised to 28 C		
24 hr after injection	98[c]	90–100
at first deaths[b]	77[c]	40–100
96 hr after injection	76[c]	40–100

[a]Significantly lower than for constant 28 C ($P = 0.05$).
[b]At 64–72 hr after injection in fish held at 28 C.
[c]Significantly higher than for constant 19 C ($P = 0.05$).

In a separate study, a group of 3.1 g channel catfish were each injected with 0.1 ml of HBSS. Aquaria were stocked with 10 injected fish each and duplicate aquaria were treated with each temperature regime (previously described) except that temperature change was not effected at 96 hr after injection. Mortality was 5% when the temperature was reduced to 19 C at 24 hr after injection, and 0 in each of the other tests.

The percentages of mortality were transformed to arc-sine percentages and compared by an analysis of variance using Dunnett's test ($P = 0.05$) (Steel and Torrie 1960).

Results — The mean percentage mortality of virus infected fish held at 28 C was 94% (Table 1). When the temperature was reduced to 19 C at 24 hr after injection, the percentage of mortality was significantly reduced to 24%. Temperature reduction when first deaths occurred did not significantly reduce the percentage of mortality below that at the constant 28 C.

The mean percentage of mortality of infected fish held at 19 C was 14%.

The percentage of mortalities of the three groups for which the temperature was raised to 28 C (76–98%) was significantly higher than that of the 19 C group.

Discussion — The effects of high temperature on the development of CCVD were clearly evident in this study. Reduction of water temperature is a feasible approach to reducing the detrimental

effects of CCVD under experimental conditions and it may prove to be beneficial at catfish fingerling hatcheries where a cool water supply is available throughout the summer. The only significant reduction in mortality occurred when temperature was lowered 24 hr after injection, but in most cases CCV is not suspected until clinical signs appear and deaths occur. However, the average mortalities in the groups where the temperature was reduced at the first deaths (and after) were 16–26% less than those for the constant 28 C group. This may indicate some benefit in reducing the temperature after the disease is apparent. The results were obtained under experimental conditions where all of the fish were injected at the same rate and time, and may differ from those in natural infections. In natural infections only a few individuals may be carriers of the virus and these transmit the infection by contact or through the water to healthy fish. If the temperature is reduced when deaths appear in natural epizootics, and before a large percentage of the uninfected fish contract the virus, a much greater reduction in mortality may be realized.

The relatively high percentage of mortality after the temperature was raised to 28 C at 64–72 hr and 96 hr after injection would indicate that a subclinical infection occurred at the lower temperature, or that injected virus was retained by the fish at the lower temperature. That the percentage of mortality of these two groups was 21–22% less than for the group raised to 28 C 24 hr after injection may indicate a trend. This may have some therapeutic value in holding suspect CCV infected fish at a suboptimal temperature that would allow them to build resistance to the virus, thus rendering them less susceptible to the disease if higher temperatures were later encountered.

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An Outbreak of Redmouth Disease in Rainbow Trout (*Salmo gairdneri*) in Saskatchewan

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During 1972 an outbreak of disease due to the "RM bacterium" occurred in caged rainbow trout (*Salmo gairdneri*) in a southern Saskatchewan lake. The mortality rate was approximately 1% of the population per week. Histopathologic lesions involved primarily the hematopoietic and reticuloendothelial systems. It is postulated that the disease was introduced with shipments of trout imported from Idaho shortly before the outbreak.

WOBESER, G. 1973. An outbreak of redmouth disease in rainbow trout (*Salmo gairdneri*) in Saskatchewan. J. Fish. Res. Board Can. 30: 571–575.

Il se produisit en 1972 une épidémie de la maladie bactérienne de la bouche rouge ("bactérie RM") chez des truites arc-en-ciel (*Salmo gairdneri*) encagées dans un lac du sud de la Saskatchewan. Le taux de mortalité fut approximativement de 1% de la population par semaine. Les lésions histopathologiques affectent surtout les systèmes hématopoiétique et réticuloendothélial. On croit que la maladie a été introduite par des truites arc-en-ciel importées de l'Idaho et arrivées peu de temps avant le début de l'épidémie.

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REDMOUTH disease (RMD) has apparently not been previously reported in Canada. The disease had been diagnosed in rainbow trout (*Salmo gairdneri*) in Idaho, Colorado, Nevada, California, and Arizona (Rucker 1966), and is enzootic in some areas of Idaho (M. Beck personal communication)[1]. The disease is caused by the "RM bacterium", which was characterized by Ross et al. (1966). Although RMD is a potentially serious disease and occurs in areas from which trout are imported into Canada, the disease is not considered under the present Canadian Salmonidae Import Regulations (Department of Fisheries and Forestry of Canada 1971).

The history, clinical signs, pathologic lesions, and bacteriologic findings in an outbreak of RMD in rainbow trout in Saskatchewan are described.

History — In July 1971 150,000 rainbow trout fingerlings imported from Montana were stocked in cages in a small lake in southern Saskatchewan. Samples of these fish were examined for disease in this laboratory on three occasions (July, October, and December 1971) with no evidence of RMD being observed. In May 1972 the number of these fish remaining in the lake had been reduced by sales and mortality to about 100,000. The surviving fish ranged from approximately 15 to 22 cm in length. In 1972 further importations of rainbow trout were made from one supplier in Idaho as follows:

Date	Average length of fish (*cm*)	Quantity
Apr. 19	5	100,000 fish
	7.5	120,000 fish
May 2	10	2000 lb
May 13	7.5	2500 lb

These fish were held in cages immediately adjacent to the 15–22 cm fish. The normal daily mortality among the 100,000 15–22 cm fish was 3 or 4 fish. On May 23 approximately 50 dead fish were found in the cages and on May 24 more than 75 sick or dead fish were observed. The sick fish were darker than normal, sluggish, and exopthalmus was observed in some. Mortality was confined to this size of fish but occurred throughout the cages containing these fish. Water temperature at this time was approximately 17 C. By May 31 the cumulative mortality reached approximately 1000 fish or 1% of the population.

Materials and methods — Samples of fish were submitted to the laboratory, on three occasions (Table 1),

[1]Dr Milton Beck, Buhl, Idaho, is an authorized certifying official as required under the Canadian Salmonidae Import Regulations.

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TABLE 1. Numbers of moribund[a] and apparently normal 15–22-cm trout with gross lesions.

Lesion	May 24 6 moribund fish	May 39 10 moribund fish	May 31 7 apparently normal fish
Petechial hemorrhage in			
oral cavity	3	4	0
fin base	2	7	1
sclera	2	6	0
swim bladder	6	9	0
muscle	0	4	0
distal intestine (serosa)	2	6	0
peripancreatic region	6	10	0
myocardium	1	1	0
gill filament	0	2	0
liver	1	6	0
gonad	0	2	0
Spleen swollen and congested	6	10	0
Watery stomach contents	3	9	0
Clear yellow mucus in intestine	6	10	0
Exopthalmus	0	3	0
Skin darker than normal	6	5	0
Corneal opacity	0	2	0

[a]RM bacterium isolated from these fish.

in water in 20-liter plastic bags surrounded by ice. The fish were examined visually, then anesthetized with tricaine methanesulfonate.[2] The caudal peduncle was severed and blood samples were collected in heparinized microhematocrit tubes.[3] These tubes subsequently were centrifuged and the packed cell volume (PCV) and the total protein (TP) content of the plasma was determined.[4] Following collection of blood samples the fish were killed by severing the spinal cord caudal to the head.

Trypticase soy agar (TSA) plates incubated at room temperature (approximately 23 C) were used for primary isolation from the anterior kidney. Representative colonies were subcultured on TSA and standard microbiological methods were used for the following tests: motility, hydrogen sulfide, indole, urease, and nitrite (Cowan and Steel 1966). Carbohydrate utilization was determined in phenol red broth base with 0.5% NaCl. Cytochrome oxidase was tested for with Pathotec test papers.[5] Flagella were demonstrated by the use of modified Leifson stain.[6] Sensitivity to antibiotics was determined using discs[7] containing the following concentrations of antibiotics placed on heavily inoculated TSA plates: kanamycin (30 μg), tetracycline (30 μg), dihydrostreptomycin (10 μg), furacin (100 μg), triple sulfa (1 μg), chloramphenicol (30 μg), and penicillin (10 μ).

Tissues collected for histopathology (liver, anterior and posterior kidney, spleen, stomach, intestine, and the entire head with the brain exposed) were immersed in Bouin's fixative for 24 hr, postfixed in 70% alcohol until trimmed, processed by routine methods, and stained with hematoxylin-eosin.

TABLE 2. Numbers of trout from which RM bacterium was isolated.

Date submitted	Length	Isolations	Remarks
May 24	15–22 cm	6/6[a]	gross lesions
May 29	15–22 cm	10/10	gross lesions
	10 cm[b]	2/6	gross lesions
	7.5 cm[b]	4/7	all grossly normal
May 31	15–22 cm	0/7	all grossly normal
	7.5 cm[b]	5/10	1 isolation from a normal fish

[a]Number of fish examined.
[b]Fish imported from Idaho in 1972.

[2]Fraser Medical Supplies Ltd., Vancouver 6, B.C.
[3]Capilets, B 4415–2-Canadian Laboratory Supplies Ltd., Toronto 18, Ont.
[4]AO TS Refractometer, AO Instruments Co., Buffalo, N.Y.
[5]Warner-Chilcott, Morris Plains, N. J.
[6]Becton-Dickson and Co. Ltd., Clarkson, Ont.
[7]Sensi-disc, Becton-Dickson and Co. Ltd., Clarkson, Ont.

Gross pathology — Splenomegaly and the presence of excessive amounts of clear yellow mucus in the intestine were observed in all of the moribund 15–22 cm fish examined (Table 1). Petechial hemorrhages in individual organs were less consistently found; however, hemorrhage in one or more sites was present in each of these fish. Other lesions occurred with varying frequency.

Hematology — The mean PCV and TP values for the 15–22 cm fish submitted on the three occasions were as follows:

Date	Packed cell volume (%)	Total protein (*g/100 ml*)
May 24 (6 moribund fish)	24.8(17.0–33.5)[8]	3.5(1.9–4.2)
May 29 (10 moribund fish)	21.5(14.0–38.0)	2.4(0.8–3.2)
May 31 (7 apparently normal fish)	46.1(40.0–51.0)	4.7(3.5–5.6)

[8]Range.

Bacteriology — A bacterium was isolated from the anterior kidney of all moribund 15–22 cm fish and also from both apparently healthy and diseased Idaho fish (Table 2). The biochemical reactions and other characteristics of the bacterium were very similar to those of the RM bacterium described by Ross et al. (1966), Table 3. The organism was sensitive to all antibiotics except penicillin at the concentrations tested. A subculture of the organism sent to R. A. Busch, University of Idaho, was found to be antigenically identical with the RM bacterium composite maintained in that laboratory and biochemically very similar to isolates from several areas of Idaho.

Four rainbow trout 12–18 cm in length from a group being held in the laboratory for other purposes were inoculated intraperitoneally with 0.1 ml of a saline suspension of culture containing approximately 1×10^{10} organisms/ml. Three of the four fish died between 50 and 60 hr post inoculation (pi). The fourth fish was moribund and killed at 62 hr pi. The lesions seen in these fish were essentially the same as those seen in the natural cases with the addition of the presence of serosanguinious ascitic fluid. The organism was re-isolated from the anterior kidney of all four fish. Two fish injected with 0.1 ml of sterile saline at the same time and placed in the same container became sluggish and dark in color 135 hr pi (i.e. 73 hr after the removal of the last fish inoculated with the organism). Gross lesions observed in these fish were identical to those seen in the natural cases, and the organism

TABLE 3. Comparison of characteristics of present isolate and RM bacterium after 2 days incubation.

Test or substrate	Present isolate (23 C)	RM bacterium (22 C) Ross et al. 1966
Gram stain	–	–
Morphology	rod shaped	rod shaped
Flagellation	peritrichous	peritrichous
Hydrogen sulfide	–	–
Motility	+	+
Cytochrome oxidase	–	–
Nitrite	+	+
Indole	–	–
Urease	–	–
Pigment on TSA	–	–
Glucose	A[a]	A
Lactose	–	–
Sucrose	–	–
Sorbitol	–	–
Arabinose	A	–[b]
Raffinose	–	–
Rahmnose	–	–
Maltose	AG[c]	AG

[a]A-Acid.
[b]Negative at 22 C, weak positive after 1–2 days at 37 C.
[c]AG. Acid plus gas production.

was isolated from the anterior kidney of both fish. Two fish injected with 0.1 ml of sterile saline at the same time and maintained in another container did not become ill and bacteria were not isolated from these fish when examined 135 hr pi.

Histopathology — The histopathologic lesions observed in fish from which the RM bacterium was isolated involved primarily the hematopoietic and reticuloendothelial (RE) systems (Table 4). In both the anterior and posterior kidney there was a severe loss of hemapoietic tissue, due to necrosis, together with dilation of sinusoids, decrease in size and numbers of pigment cells, and swelling and vacuolation of RE cells (Fig. 1–4). Nephrons in the posterior kidney did not appear to be altered. In the spleen there was a total loss of the normal lymphoid follicular structure, congestion of the sinusoids with erythrocytes, and RE cell hypertrophy. In the livers of the apparently healthy fish, vacuolation of hepatocytes was prominent (Fig. 5), while few or no vacuoles were present in the hepatocytes of diseased fish (Fig. 6). The RE cells lining the hepatic sinusoids of diseased fish were swollen and prominent with vesicular nuclei (Fig. 6). Very marked accumulations of mononuclear cells were present in the periportal areas of livers of diseased fish (Fig. 7–8). The identity of these cells was impossible to determine in the tissue sections, but many resembled lymphocytes. Mitotic figures were not uncommon among these cells, indicating proliferation of existing lymphoid and RE elements of the liver. Foci of necrosis, in association with pooling of erythrocytes in dilated sinusoids, produced the hemorrhages grossly visible in the livers of some fish.

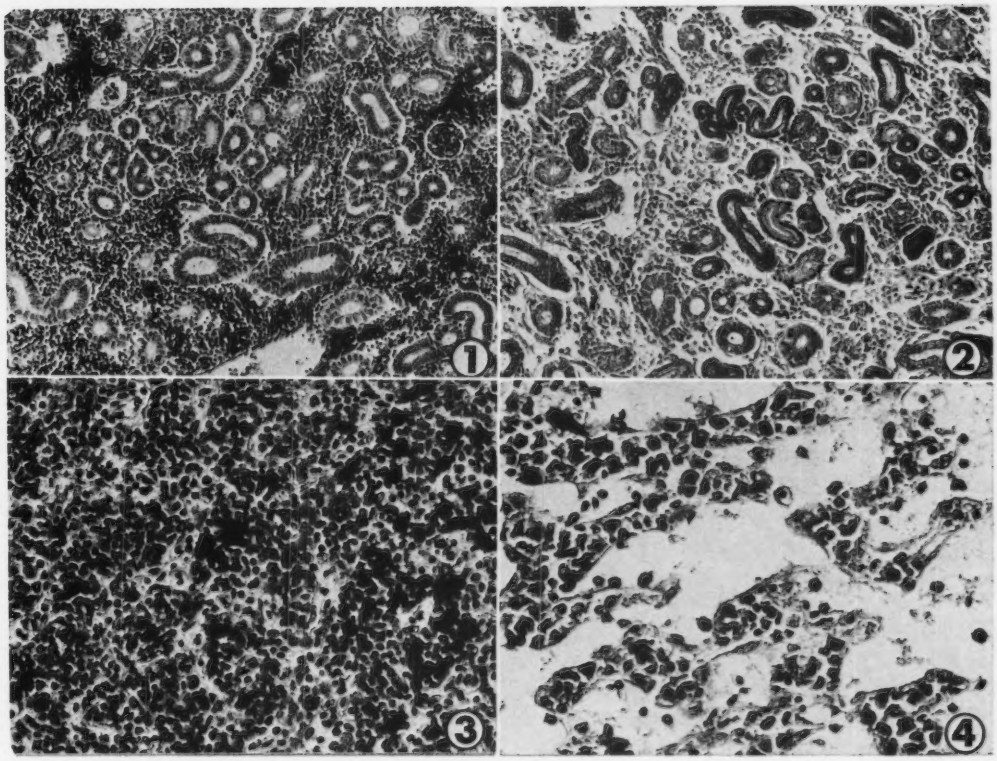
Periocular lesions were common, with retrobulbar edema being present in all of the fish from which the eyes were examined, and panopthalmitis, characterized by intraocular hemorrhage and inflammatory cell infiltration, was present in 4 of 8 fish examined. The inflammatory cells present within the eye were a mixture of polymorphonuclear leukocytes and macrophage-like cells.

Discussion — The owner initiated treatment with oxytetracylcine HCl at 3500 g/ton of feed about 1 week after the initial diagnosis was made. Although the mortality rate began to decline after 5–7 days of treatment, the treatment was changed to sulfamerazine at 200 g of sulfa/ton of feed. This was maintained for 14 days. All fish showing clinical signs of disease were removed from the cages and destroyed. Mortality returned to what was considered to be a normal level after 5 days of treatment

TABLE 4. Occurrence of histopathologic lesions in moribund 15–22 cm fish from which RM bacterium was isolated.

Organ	Lesion	Fish with lesions
Anterior kidney	Loss of hematopoietic tissue	16/16[a]
	Decrease in pigment cells	16/16
	Swelling of RE cells	16/16
	Perirenal edema	7/16
	Perirenal hemorrhage	3/16
Posterior kidney	Loss of hematopoietic tissue	16/16
	Decrease in pigment cells	12/16
	Swelling of RE cells	16/16
Liver	Periportal lymphoid cell accumulation	14/15
	RE cell activation	13/15
	Focal necrosis	8/15
	Hemorrhage	6/15
Pyloric caeca	Submucosal edema	3/15
Intestine	Submucosal edema	12/13
	Subserosal hemorrhage	3/13
Spleen	Loss of lymphoid follicles	16/16
	Congestion	16/16
	Swelling of RE cells	16/16
Thymus	Focal necrosis	4/14
Heart	Myocardial hemorrhage	1/11
Eye	Retrobulbar edema	8/8
	Retrobulbar hemorrhage	7/8
	Panopthalmitis	4/8

[a]Number of fish examined.



FIGURES 1–4

FIG. 1, 2. Posterior kidney of apparently healthy fish and moribund fish from which RM bacterium was isolated, respectively. Hematoxylin-eosin. × 113. 1, Diffuse cellularity of hematopoietic tissue in interstitial areas, and pigment cells in clusters; 2, marked reduction of hematopoietic tissue and pigment cells. Renal tubules apparently unaffected. FIG. 3, 4. Anterior kidney of apparently healthy fish and moribund fish from which RM bacterium was isolated, respectively. Hematoxylin-eosin. × 285. 3, Dense accumulation of hematopoietic tissue surrounding sinusoids; 4, reduction of hematopoietic tissue, dilation of sinusoids, and swelling of individual remaining cells.

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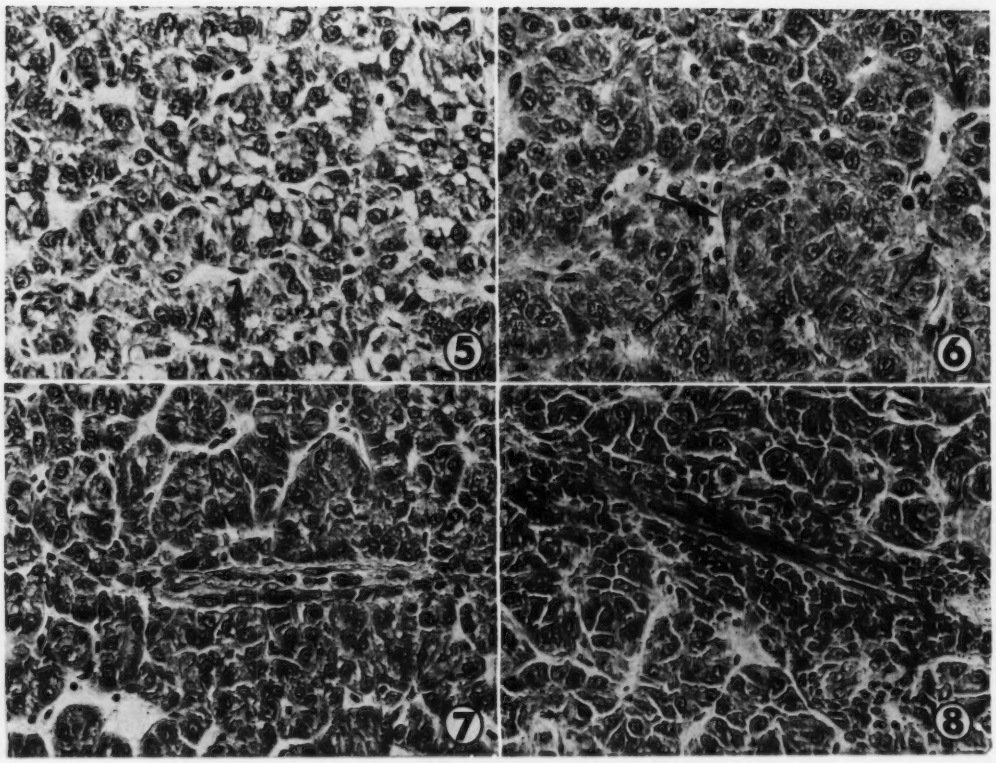

FIGURES 5–8

FIG. 5, 6. Liver of apparently healthy fish and moribund fish from which RM bacterium was isolated, respectively. Hematoxylin-eosin. × 330. 5, Extensive vacuolation of cytoplasm of hepatocytes. Small, unconspicuous RE cell lining sinusoid (arrow); 6, cytoplasm of hepatocytes granular, cytoplasm with no intracytoplasmic vacuoles. RE cells very prominent and enlarged with pale granular nuclei (arrows). FIG. 7, 8. Portal area of liver of apparently healthy fish and moribund fish from which RM bacterium was isolated, respectively. Hematoxylin-eosin. × 315. 7, Vacuolation of cytoplasm less marked than in Fig. 5; 8, extensive perivascular accumulation of lymphoid cells in portal area.

with sulfamerazine. There was no increase in mortality following cessation of treatment and further treatment was not required.

In general, it appears that the histopathologic lesions of RMD have little specificity, stressing the need for isolation and identification of the causative organism. The destruction of hematopoietic tissue in the kidney and spleen is a lesion common to a number of viral diseases of trout (Yasutake 1970) and has also been described in furunculosis (Klontz et al. 1966). Focal hepatic necrosis is also a feature of some viral diseases (Yasutake 1970), but the periportal accumulation of lymphoid cells seen in the present disease is not a feature of those diseases. The relation of this lesion to the increase in "lymphocytopoietic activity in the liver..." described in furunculosis by Klontz et al. (1966) is unclear.

The absence of vacuoles in the hepatocytes of moribund fish may represent glycogen depletion. The presence of these vacuoles, which have been shown to be composed of glycogen (Scarpelli 1967; Hinton et al. 1972), is regarded as normal in rainbow trout (Wales 1970). The anemia observed in these fish was likely the result of hemorrhage together with insufficient replacement due to hematopoietic tissue damage.

Although the transmission experiment was very limited, it did demonstrate the pathogenicity of the organism for rainbow trout and the transmission of the organism, probably through the water, from inoculated to contact fish. Rucker (1966) showed water transmission of RMD, and the minimum incubation period of 5 days was similar to that found in the present case.

It appears likely that the disease was introduced with the trout imported from Idaho. The disease to the author's knowledge has not been reported from Montana where the 15–22 cm trout orginated, and there had been no disease problem noted in the large fish until about May 23, 1972. Routine examination, including bacteriology, of three samples of fish from the lake prior to the introduction of the Idaho fish had not revealed the presence of RMD. The premises in Idaho from which the fish were imported was known to have had RMD (M. Beck personal communication). However, under the present Salmonidae Import Regulations this did not affect the suitability of the fish for importation.

The isolation of the organism from apparently normal Idaho fish suggested that these fish might have been asymptomatic carriers. The carrier state was experimentally produced by Rucker (1966) in fish exposed to RM bacterium.

Some confusion exists with regard to RMD, since similar bacterial septicaemias due to *Aeromonas*, *Pseudomonas*, and *Vibrio* spp. also are referred to by this name. Since some of these other organisms are ubiquitous in distribution, it is vital that the etiologic agent be specified when a diagnosis of RMD is made. The author fully supports the recommendation made by Rucker (1966) that the term "redmouth disease" be reserved for infections due to RM bacterium.

The significance of this outbreak of RMD for rainbow trout culture in Canada is unknown at the present time; however, this case illustrates that diseases other than those presently specified under the Canadian Salmonidae Import Regulations should be considered before importation is permitted, and that the importation of fish potentially carrying any disease not known to occur in Canada is a highly questionable practice.

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Optimal Control Theory Applied to a Dynamic Aquatic Ecosystem

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In this report we present a dynamic model for an aquatic ecosystem consisting of a single species living in a polluted environment. Considering the dynamics of growth of the species and increase in pollution, we apply optimal control theory to obtain species removal and pollution reduction rates at minimum cost.

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Nous présentons dans cet article un modèle dynamique d'un système écologique consistant en une espèce unique habitant un milieu pollué. Tenant compte de la dynamique de la croissance de l'espèce et du niveau de pollution, nous appliquons des techniques de contrôle optimal, en vue d'obtenir les résultats désirés avec un minimum de coût.

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THE system considered in this report is governed by two coupled differential equations, one describing the dynamic behavior of the population growth of a biological species (e.g. of a fish population, like salmon) in the presence of an hostile environment, like increasing pollution, and another describing the increase in pollution level. By introducing control variables for the rate of removal of the species (for possible human consumption) and the rate of pollutant decrease, we formulate two optimal control problems. The forms of the optimal control policies are obtained by using well-known optimization techniques for dynamical systems. The results can be easily extended to multi-species populations and they apply directly to current fisheries problems.

Dynamic model of an ecosystem — The dynamic behavior of the population growth of a biological species is described by the equation

$$(1)\quad \frac{dN}{dt} = [a - bN(t) - \int_{-\infty}^{t} K(t,s)\ N(s)ds - P(t)]N(t)$$

where $a > o$ is the coefficient of reproduction rate combined with death rate, $b > o$ is the coefficient of inhibition taking care of competition within the species for food and other necessities for survival, $K(t,s) \geq 0$ is the coefficient of species self-intoxication (Volterra et d'Ancona 1935), and the quantity $\int_{-\infty}^{t} K(t,s)\ N(s)ds$ is the total buildup up to the time t due to the population history $\{N(s): -\infty < s \leq t\}$; $N(t)$ is population density and $P(t)$ is the pollution level at time t caused by disposal of industrial and city waste up to t.

The short-term effect of pollution on the species is the decline in its population due to death caused by intoxication and the long-term effect is again decline in population growth.

The quantity $P(t)$ may be measured in the units of pollutant content (such as Hg, Phosphate, Nitrogen, etc.) per unit weight (or volume) of water. In a dynamic society the increase in pollution depends in a very complex way on technological, industrial, and political development and on the network of rivers, lakes, and artificial water reservoirs. It will be assumed that this is described by a single differential equation:

$$(2)\quad \frac{dP}{dt} = f(t,\ P(t),\ \int_{-\infty}^{t} K(t,s)\ N(s)\ ds)$$

where f is mainly determined by the factors mentioned above. The function f is shown to depend explicitly on time t to take into account any ecological changes that may be brought about by technological development.

It is clear that the system of equations 1 and 2, called the ecosystem S, describes the dynamics of the ecology consisting of a biological species (like fish) struggling to survive in a polluted environment.

The increase in pollution influences the growth of the species (N) and, as shown by Volterra and d'Ancona (1935), if the system S is left to itself without external control, the species may face extinction, grow unbounded, or attain an equilibrium.

In this report we are concerned with the external control of system S. The control on the system may be effected by different technical means. Without making any distinction of the technical means applied, we will assume that control can be exerted so as to reduce the rate of increase in pollution. This control may be called

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the pollution reduction rate, $v(t)$. This control is constrained due to limitation of available scientific and technical means of reduction. We may assume without any loss of generality that $0 \leq v(t) \leq 1$, since if $0 \leq v(t) \leq \epsilon$ finite, then the P equation may be divided by the factor ϵ throughout.

For human consumption, species removal (e.g. fishing) may be allowed at a certain functional rate, say $u(t)$ $(0 \leq u(t) \leq h < 1)$ at time t. Consequently system S will appear as

$$(3)\quad \begin{cases} \dfrac{dN}{dt} = [a - b\,N(t) - \displaystyle\int_{-\infty}^{t} K(t,s)\ N(s)ds - P(t) \\ \qquad - u(t)]\,N(t) \\ \dfrac{dP}{dt} = f(t,\ P(t),\ \displaystyle\int_{-\infty}^{t} K(t,s)\ N(s)ds) - v(t) \end{cases}$$

The dynamics of the complete ecological system under the influence of external controls (u, v) is described by the system of equations 3. It is intuitively clear that by a judicious choice of the control pair (u,v) it may be possible not only to prevent extinction of the species but also to guarantee a permanent source for human consumption.

In the following section we formulate some control problems involving the system 3.

Physically meaningful performance criteria and associated control problems — We shall consider the ecosystem 3 in the time interval $0 \leq t \leq T_1$, where T_1 is either a fixed time or a time at which a particular objective is met. Without any loss of generality we can assume that $0 \leq u(t) \leq h < 1$ and $0 \leq v(t) \leq 1$. The initial conditions at $t = 0$ are assumed to be known.

Suppose that a given removal rate of the species (N) is required by time T_1 (given). This imposes the following additional constraint on the selection of the control u:

$$(4)\qquad \int_0^{T_1} u(t)\ N(t)\ dt = C,\ (C,\ T_1 \text{ given}).$$

Let us consider first the case where there is no pollution control i.e. $v \equiv 0$. The performance of the system 3 may be then measured by the profit criterion

$$(5)\quad J\ [u] = \int_0^{T_1} C_0(t)\,u(t)\,N(t)\,dt - \int_0^{T_1} C_1(t)\ u(t)\ dt$$

where $C_0(t)$ is an index of unit profit arising from removal of species N and $C_1(t)$ a cost index of the control policy $u(t)$.

If, however, there is pollution control and $C_2(t)$ is an index of its cost then the performance criterion considered is

$$(6)\quad J\ [u,v] = \int_0^{T_1} C_0(t)\ u(t)\ N(t)\ dt - \int_0^{T_1} C_1(t)\ u(t)dt - \int_0^{T_1} C_2(t)v(t)dt$$

We shall study below the following optimal control problems:

P_1: Find a control policy $u \in L_\infty$, $0 \leq u(t) \leq h$, such that the system 3, without pollution control (i.e., $v \equiv 0$), will achieve its goal (4) while maximizing the net profit (5).

P_2: Find control policies $u,v \in L_\infty$, $0 \leq u(t) \leq h$, $0 \leq v(t) \leq 1$, such that the system 3, with pollution control considered, will achieve the objective (4) while maximizing the net profit (6).

Remark: The solution of problem P_1 cannot be obtained from the one of problem P_2, despite the fact that (5) is a special case of (6).

Optimal control policy — Before proceeding to the optimization problems it will be convenient to introduce a uniform notation of state and control variables:

$$(7)\quad \begin{array}{lll} x^1(t) \triangleq N(t) & & w^1(t) = u(t) \\ x^2(t) \triangleq P(t) & & w^2(t) = v(t) \\ x^3(t) \triangleq & \displaystyle\int_0^t u(s)\ N(s)\ ds & \end{array}$$

The state variable x^3 was introduced in order that we incorporate the constraint (4) into the dynamic equations (3). We thus obtain the system:

$$(8)\quad \begin{cases} \dfrac{dx^1}{dt} = [a - bx^1(t) - \displaystyle\int_{-\infty}^{t} K(t,s)x^1(s)\ ds\text{-}x^2(t) \\ \qquad - w^1(t)]x^1(t) \\ \dfrac{dx^2}{dt} = f(t,\ x^2\ (t),\ \displaystyle\int_{-\infty}^{t} K(t,s)x^1\ (s)\ ds) - w^2(t) \\ \dfrac{dx^3}{dt} = w^1(t)x^1(t) \end{cases} \quad t \in [0,T_1]$$

with $x^1(0) = N(0)$, $x^2(0) = P(0)$, $x^3(0) = 0$, $x^1(t) = \phi(t)$, $t \in [-\infty, 0)$ where $N(0)$, $P(0)$, and $\phi(t)$ are assumed to be known. It is also given from (4) and (7) that $x^3\ (T_1) = C$.

Let the performance criterion of system 8 be:

$$(9)\quad J\ [w^1, w^2] = \int_0^{T_1} f^0(x^1(t),\ x^2(t),\ w^1(t),\ w^2(t),t)\ dt$$

and let us define the target manifold

$$(10)\qquad S_1 = \{(x^1, x^2, x^3) \in E^3 : x^3 = C\}$$

We shall try to reduce system 8 to a simple dynamical system which can be treated by Pontryagin's maximum principle (1962, p. 19). We thus consider two cases: i) $K \equiv 0$, and ii) $K \not\equiv 0$.

(i) *$K \equiv 0$ i.e. the effect of species self-intoxication is negligible compared with the external pollution* — The Hamiltonian (Pontryagin 1962, p. 18) of the system is

$$(11)\quad \hat{H} = -f^0 + \psi_1[a - bx^1 - x^2 - w^1]x^1 + \psi_2[g(t,x^2) - w^2] + \psi_3\ w^1x^1$$

where $g(t,z) \triangleq f(t, z, 0)$ and the auxiliary variables ψ_1, ψ_2, ψ_3 satisfy system 12 adjoint to system 8:

$$(12)\quad \begin{cases} \dfrac{d\psi_1}{dt} = \dfrac{\partial f^0}{\partial x^1} - (a - 2bx^1 - x^2 - w^1)\,\psi_1 - w^1\psi_3 & ,\psi_1(T_1) = 0 \\ \dfrac{d\psi_2}{dt} = x^1\psi_1 - \dfrac{\partial g(t,x^2)}{\partial x^2}\,\psi_2 & ,\psi_2(T_1) = 0 \\ \dfrac{d\psi_3}{dt} = 0 & ,\psi_3(T_1) = d \neq 0 \end{cases}$$

We can now consider the two problems mentioned in the previous section:

P_1: In this case $f^0(x^1,x^2,w^1,w^2,t) = -(C_0w^1x^1 - C_1w^1)$, $w^2 \equiv 0$, and from (11) and the well-known Pontryagin's Maximum Principle we obtain that the optimal control policy must be of the form:

$$(13)\quad w^1(t) = \frac{h}{2}\left\{1 + \operatorname{sgn}\left[C_0x^1 - C_1 - \psi_1x^1 + \psi_3x^1\right]\right\} \quad ,t \in [0, T_1]$$

where sgn $(\cdot)$ is the signum function.

P_2: In this case $f^0(x^1,x^2,w^1,w^2,t) = -(C_0w^1x^1 - C_1w^1 - C_2w^2)$ and similarly from (11) and the Maximum Principle one obtains that the optimal control policies must be of the form:

$$(14)\quad \begin{cases} w^1(t) = \dfrac{h}{2}\left\{1 + \operatorname{sgn}\left[C_0x^1 - C_1 - \psi_1x^1 + \psi_3x^1\right]\right\} & ,t \in [0, T_1] \\ w^2(t) = \dfrac{1}{2}\left\{1 + \operatorname{sgn}\left[-C_2 - \psi_2\right]\right\} \end{cases}$$

Remark: As shown from (13) and (14) the optimal species removal rate and pollution control may be zero over certain intervals of time.

(ii) *$K \not\equiv 0$ i.e. the effect of species self-intoxication is not negligible compared with the external pollution* — Assuming that $K(t,s)$ is continuous in both arguments and that $K(t,s) = K(t-s)$, we can approximate it with a series of exponentials i.e. $K(t) = \sum_{i=1}^{M} \alpha_i\, e^{-\gamma_i t}$. In this way the hereditary system (8) can be easily reduced to a simple dynamical one. To demonstrate this let us assume that $K(t) = \alpha\, e^{-\gamma t}$. We define now a new state variable:

$$(15)\quad x^4(t) = \alpha \int_{-\infty}^{t} e^{-\gamma(t-s)}\, N(s)\, ds \text{ and}$$

$$(16)\quad \frac{dx^4}{dt} = -\gamma x^4(t) + \alpha x^1(t), \text{ with } x^4(0) = \alpha \int_{-\infty}^{0} e^{\gamma s}\, \phi(s)\, ds$$

where $\phi(t)$ is the past history of the species N.

Thus system 8 reduces to the dynamical (but augmented) system:

$$(17)\quad \begin{cases} \dfrac{dx^1}{dt} = [a - bx^1(t) - x^4(t) - x^2(t) - w^1(t)]\,x^1(t) & ,x^1(0) = N(0) \\ \dfrac{dx^2}{dt} = f(t, x^2(t), x^4(t)) - w^2(t) & ,x^2(0) = P(0) \\ \dfrac{dx^3}{dt} = w^1(t)\,x^1(t) & ,x^3(0) = 0 \\ \dfrac{dx^4}{dt} = \alpha x^1(t) - \gamma x^4(t) & ,x^4(0) = \alpha \displaystyle\int_{-\infty}^{0} e^{\gamma s}\,\phi(s)ds \end{cases}$$

The target manifold of the system is now

$$\hat{S}_1 = \left\{(x^1, x^2, x^3, x^4) \in E^4 : x^3 = C\right\}.$$

Since equation 16 does not contain explicitly the control variables w^1 and w^2, the forms (13 and 14) of the optimal control laws found in the case $K \equiv 0$ will remain unchanged. But the adjoint variables ψ_i, $i = 1,2,3,4$ will satisfy now the augmented system

$$(18)\quad \begin{cases} \dfrac{d\psi_1}{dt} = \dfrac{\partial f^0}{\partial x^1} - (a - 2bx^1 - x^4 - x^2 - w^1)\,\psi_1 - w^1\,\psi_3 + \alpha\psi_4, & ,\psi_1(T_1) = 0 \\ \dfrac{d\psi_2}{dt} = x^1\psi_1 - \dfrac{\partial f\,(t,x^2,x^4)}{\partial x^2}\,\psi_2 & ,\psi_2(T_1) = 0 \\ \dfrac{d\psi_3}{dt} = 0 & ,\psi_3(T_1) = d \neq 0 \\ \dfrac{d\psi_4}{dt} = +x^1\psi_1 + \gamma\psi_4, & ,\psi_4(T_1) = 0. \end{cases}$$

Similarly, if $K(t) = \sum_{i=1}^{M} \alpha_i e^{-\gamma_i t}$ system 8 will be reduced to a dynamical system of order (M+3), the adjoint system will be also of dimension (M+3), but the form of the optimal control policies will be still given by (13) (for Problem P_1) and (14) (for Problem P_2).

Computational procedure — To solve control problems P_1 and P_2 explicity one should solve the adjoint system backwards in time, obtain the solutions as functions of the yet unknown terminal condition d, substitute in (13 or 14), obtain the control as a function of d, substitute in dynamical equations (8), solve system 8 in the fixed interval $[0, T_1]$, and obtain the value of the unknown parameter d from the requirement that $x^3(T_1) = C$. This parameter being determined the control laws are completely determined too.

If the equation $x^3(T_1,d) = C$ does not have a real solution d then one must change the requirements of

either time T_1 (increase it) or total species removal C (decrease it) or both.

Conclusion — It is interesting to note that the expression (14) for the optimal controls suggests that both fishing and pollution removal operations are to be either carried on at the maximum capacity or be completely suspended for certain periods of time. Insight into the causes of such control policies may be gained by studying the sign changes in expression (14).

The authors hope that this report will stimulate interest in applying optimal control theory to current fisheries problems.

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Parental Age and Survival of Progeny in Splake Hybrids (*Salvelinus fontinalis* × *S. namaycush*)

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While examining the survival rates of eggs in a splake brood stock, it was found that the survival of progeny from egg to the time of yolksac absorption increased as the age of the parents increased.

Examination of spawning success of individual fish in another brood stock indicated that the increased survival rate was related to the female parent. There was no effect of the female parent on survival from eggs to eyed eggs, but there was a significant effect of survival from eyed eggs to hatch and from hatch to the time of yolksac absorption.

AYLES, G. B., AND A. H. BERST. 1973. Parental age and survival of progeny in splake hybrids (*Salvelinus fontinalis* × *S. namaycush*). J. Fish. Res. Board Can. 30: 579–582.

Au cours d'observations sur la survie des oeufs d'un stock reproducteur de truites moulac, nous nous sommes rendus compte que la survie de la progéniture, depuis l'oeuf jusqu'au moment de la résorption du sac vitellin, augmentait en proportion directe de l'âge des parents.

L'évaluation du succès de la fraie d'individus d'un autre stock reproducteur indique que l'augmentation du taux de survie est liée au parent femelle. La survie de l'oeuf jusqu'au stade oculé n'est pas affectée par le parent femelle, mais elle l'est de façon significative entre le stade d'oeuf oculé et l'éclosion, et entre l'éclosion et le stade de résorption du sac vitellin.

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SINCE 1957, the Ontario Ministry of Natural Resources has conducted a research program on the selective breeding of hybrids of brook trout (*Salvelinus fontinalis*) and lake trout (*S. namaycush*) for planting in the Great Lakes (Budd 1957; Christie 1960; Fry 1961; Berst and Spangler 1970; Tait 1970). The program has involved the selection of hybrids through several generations for sexual maturity by age III and ability to live in deep water. Plantings of progeny of selected splake stocks are being made in Lake Huron in order to establish self-sustaining populations for sport and commercial fisheries.

This study provides information on the early survival of splake which is of immediate interest to agencies concerned with the trout rehabilitation program on the Great Lakes, from the standpoints of the production and survival of progeny from parent stocks in the hatchery.

Experimental procedures — Survival data on the incubation of eggs of individual matings of F_2, F_3, and F_4 parent splake were obtained from records maintained at the fish genetics laboratory of the Research Branch of the Ontario Ministry of Natural Resources at Maple (Stock A). Survival data from Stock B, a production stock consisting of a mixed lot of F_3, F_4, and F_5 parent fish at ages III, IV, and V, were obtained from weekly records of the Provincial Fish Hatchery at Chatsworth, Ontario (mass matings).

The brood stocks were spawned artificially, each year during 1968–70 inclusive, in the period October 1 to December 15. The fish were not fed during the spawning period. The dry method of spawning was used exclusively (e.g. Leitritz 1959).

For Stock A, each lot of eggs (one female × one male per lot) was incubated at 9 ± .7 C in an individual tray and dead eggs and alevins were removed two to three times per week. Mortalities were recorded for individual crosses as either pre- or post-eyed stage until approximately 6 weeks after hatching when the surviving fry were counted and then removed. The percent survival was determined for uneyed eggs (pre-eyed mortalities), eyed eggs (from post-eyed mortalities prior to 56 days after fertilization), alevins (post-eyed mortalities after 56 days but prior to 84 days after fertilization), and for total survival (pre-eyed plus post-eyed mortalities prior to 84 days post-fertilization). The eyed egg stage and the alevin stage are based on the mean times to hatch (56 days) and to time of yolksac absorption or swim up (84 days) for this stock under existing conditions (personal communication Dr J. S. Tait, Department of Biology, York University).

For Stock B, the eggs from several females were pooled and fertilized. After hardening, they were disinfected by immersion in 1:2000 acriflavin for 25 min, measured volumetrically, and placed in a Heath incubator. An average of about 1 million eggs per year from 750 to 1000 female parents were collected and treated in this way during 1968–70 inclusive. During incubation (9± 1.5 C) the eggs were disinfected daily (for control of fungus) by a flush treatment of malachite green at a concentration of 1:200,000 for 1 hr. The first pick-off of eggs was made 40 days after fertilization. The eggs were then placed in trays set in raceways in the hatchery building and picked daily. The mortalities were recorded until approximately the time of yolk-sac absorption and the beginning of feeding. The percent survivals during the uneyed egg stage, during the eyed egg stage, and during the alevin stage, as well as the total survival from fertilization to time of yolksac absorption, were calculated.

Survival data of offspring of 22 females of Stock A, each of which had been spawned during at least three spawning seasons were examined using an analysis of covariance. The percent survival of offspring during each of the developmental stages was converted to degrees, using the arc sine square root conversion (Snedecor and Cochran 1967) prior to analysis. For the analysis of survival of offspring within each developmental stage the independent variable was the age of the female and the dependent variable was the survival of progeny. The mean slope and the standard error of the slope were calculated and percentages of the variance components attributable to difference between females, error, and age of females were also calculated (Bliss 1970) for each stage.

A similar analysis to determine the effect of the age of the male parent on the survival of progeny was performed on the data from the spawnings of 22 males from Stock A, which had each been spawned a number of times.

The majority of the splake which have been selected for early maturity are sexually mature in their second year. However, since eggs from first spawnings consistently had poor survival, as is ordinarily the case, all data used here were from fish 3 years of age or older.

Results — In Stock A there was a significant positive relationship between the age of females and the total survival of their progeny from fertilization to the time of yolksac absorption. This increase in survival with increase in parental age occurred during the eyed egg stage and during the alevin stage (Fig. 1).

There were significant differences between females at all stages. These differences may have been a result of environmental differences between females within a stock or a reflection of genetic differences specific to a hybrid stock. The significant age effect is in addition to the environmental or genetic effects and accounted for as much as 31% of the variance of the survival of offspring within one of the stages (alevin stage) (Table 1).

Similar analysis of Stock A males showed that there was no effect of age of males on survival of their progeny.

In Stock B a total of about one million fertilized eggs were produced annually during the three consecutive spawning seasons at ages III, IV, and V. Survival of uneyed eggs from this stock remained relatively constant for spawnings from age III, IV, and V parents (Fig. 2). Significant year-to-year in-

TABLE 1. Slopes of regression lines relating survival of progeny to age of the female parent, and estimates of the percent of total variance attributable to differences between females, to error, and to effect of age, for survival of uneyed eggs, survival of eyed eggs, survival of alevins, and total survival of progeny in Stock A.

	Uneyed eggs	Eyed eggs	Alevins	Total
Slope	1.05	4.52	6.52	5.21
S.E. of slope	±1.83	±1.61	±1.17	±1.77
Age effect	0%	11%	31%	7%
Between females	56%	23%	8%	37%
Error	44%	66%	61%	56%

creases in the survival of eyed eggs and of alevins occurred during the 3-year period. The increases in survival from the time of fertilization to the time of yolksac absorption from age III to IV and from IV to V parents were 2.4 and 8.9%, respectively.

Discussion — We have established that for these stocks there is a positive relation between the age of a female splake and the survival of her progeny during the eyed egg stage and during the alevin stage of early development. A similar observation has been made for carp in Russia (see Nikolskii 1969). It was found that the proportions of fertilized eggs and of surviving fry increased with the age of the parents and then decreased as they got very old.

The possible causes of this relation are of considerable interest but we can only speculate on them. It is known for other salmonids (Bagenal 1967; Rounsefell 1957) that older females have larger eggs and Svardson (1949) suggested and Bagenal (1969) has shown that fry from larger eggs have a higher chance of survival than those from smaller eggs. Competition for food and space between the larger and the smaller fry was considered to be the major factor in the different survival rates reported above, but in addition Frost and Brown (1967) reported that mortality was much higher among small eggs and alevins of brown trout in a hatchery. However, Fowler (1972) has shown that in one stock of chinook salmon at least, total egg

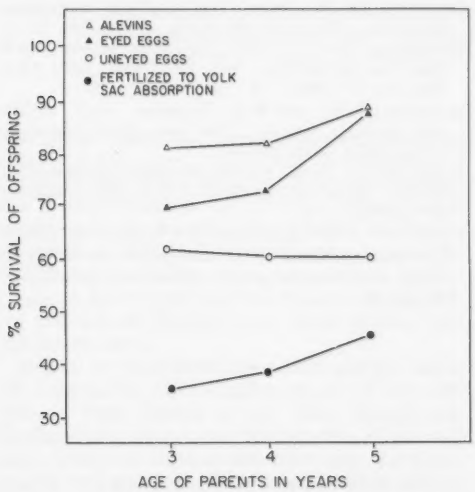

FIG. 1. Relation between the age of the female parents (Stock A) and the survival of their offspring from fertilization to swim up.

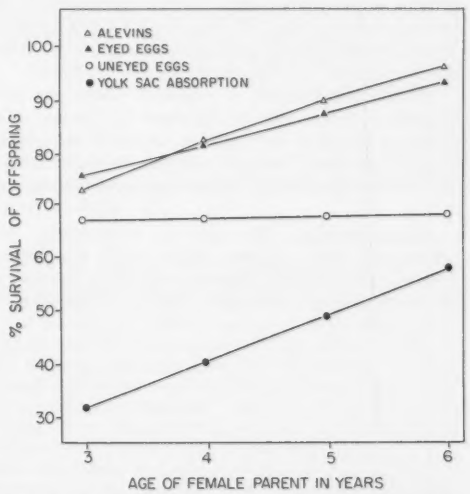

FIG. 2. Survival of eggs and fry from three consecutive years of spawning of a mixed stock of third and fourth generation brook trout × lake trout parents (Stock B).

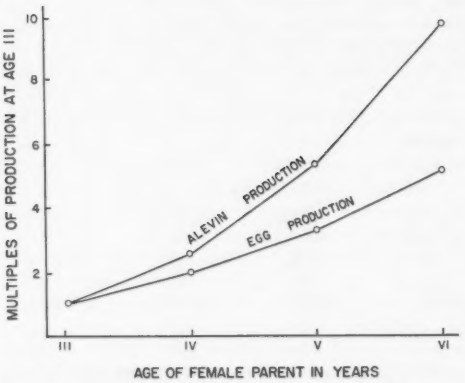

FIG. 3. Relation between the age of the female parent and the production of eggs and alevins (Stock A).

and fry mortalities were greater in offspring of females with larger eggs.

Studies on various species have shown that lipids and other components of fish eggs vary with age of the female (see Nikolskii 1969, chapter 3, for a review). The possibility exists then that older females simply produce qualitatively better eggs.

Fry production in hatcheries would be markedly affected by this age effect. The extent of this effect is shown (Fig. 3) by comparing estimates of splake egg production (Ayles 1972) and fry production (Stock A) at various ages in terms of multiples of the production at age III. There is a fivefold increase in egg production but a tenfold increase in fry production to age VI (based on Stock A results).

Further information is required before we can suggest that this relation between female age and offspring survival is common to most salvelinid populations, and not just a phenomenon restricted to these hybrid stocks from hatchery and laboratory.

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Acute and Long-Term Accumulation of Copper by the Brown Bullhead, *Ictalurus nebulosus*

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BRUNGS, W. A., E. N. LEONARD, AND J. M. MCKIM. 1973. Acute and long-term accumulation of copper by the brown bullhead, *Ictalurus nebulosus*. J. Fish. Res. Board Can. 30: 583–586.

Brown bullheads (*Ictalurus nebulosus*) were exposed to constant concentrations of copper ranging from 6.5 to 422 μg/liter. Copper concentrations in gill, opercle, liver, and kidney tissues of live fish did not differ from those that died during the acute exposure. Exposure of fish to sublethal concentrations for 20 days before exposure to lethal concentrations resulted in higher tissue levels in the dead fish than in fish not previously exposed. A distinct increase in liver and gill tissue copper concentrations occurred at exposure levels of 27 μg/liter and above. Equilibrium tissue levels of copper in the liver and gill were reached within 30 days. Copper levels in red blood cells and plasma after 20-months exposure did not differ from the controls. Red blood cells analyzed after 6-days and 30-days exposure to copper also showed no increased copper residues.

BRUNGS, W. A., E. N. LEONARD, AND J. M. MCKIM. 1973. Acute and long-term accumulation of copper by the brown bullhead, *Ictalurus nebulosus*. J. Fish. Res. Board Can. 30: 583–586.

Les auteurs ont exposé des barbottes brunes (*Ictalurus nebulosus*) à des concentrations constantes de cuivre variant de 6.5 à 422 mg/litre. Les concentrations de cuivre dans les branchies, l'opercule, le foie et le tissu rénal des poissons vivants ne diffèrent pas de celles des poissons morts au cours d'une exposition aiguë. L'exposition à des concentrations sublétales durant 20 jours précédant l'exposition aux concentrations létales produit une plus grande accumulation de cuivre dans les poissons morts que dans ceux qui n'ont pas été exposés préalablement. Il se produit une augmentation notable des concentrations de cuivre dans le foie et les branchies à des niveaux d'exposition de 27 μg/litre et plus. Dans les branchies et le foie, les niveaux d'équilibre tissulaire du cuivre sont atteints en dedans de 30 jours. Les niveaux de cuivre dans les cellules rouges sanguines et dans le plasma, après exposition de 20 mois, ne diffèrent pas sensiblement de ceux des témoins. Après exposition de 6 et de 30 jours au cuivre, les cellules rouges sanguines ne montrent pas non plus d'augmentation de résidus de cuivre.

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THE present study was conducted to determine the acute and long-term toxicity and accumulation of copper by the brown bullhead (*Ictalurus nebulosus*) and to investigate the use of copper residues as a possible autopsy procedure. In addition, an attempt was made to collect some initial information on the transport, distribution, and accumulation rate of copper in fish. Copper determinations were made for the gill, opercle, kidney, liver, blood plasma, and red blood cells.

Several autopsy procedures have proven useful for determining the causative agents of fish kills (Mount 1964; Mount et al. 1966; Mount and Stephan 1967; Brungs and Mount 1967; Mount and Boyle 1969). In these studies with zinc, cadmium, endrin, and parathion tissue concentrations differed between dead fish and living fish at a given concentration of toxicant. Therefore, a relation existed that provided an autopsy method for determining if the cause of death in a particular fish kill was one of these toxicants.

Materials and methods — Physical and Biological — The water used for all tests was a mixture of pond water, originating from a spring at the Newtown Fish Farm, an Ohio Division of Wildlife hatchery at Cincinnati, Ohio, and carbon-filtered, demineralized, tap water. The resulting mixture was maintained at a hardness of approximately 200 mg/liter (as $CaCO_3$) and was stored in an open, 400-kliter concrete reservoir. Water flowed by gravity from this reservoir to a proportional diluter (Mount and Brungs 1967). A 2-liter/concentration proportional diluter was used to deliver toxicant and water to each wooden tank (60 × 40 × 240 cm) containing 430 liters of water 30 cm deep. Water from the diluter was added to each of the six test tanks so that a calculated exchange of water took place every 12 hr. Test tanks

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TABLE 1. Chemical characteristics of the experimental water.

Characteristic	Number of analyses	Mean[a]	Range
*p*H	167	7.6±0.18	7.2–8.2
Total hardness (*mg/liter as $CaCO_3$*)	31	202±16	190–215
Alkalinity (*mg/liter as $CaCO_3$*)	165	156±10	132–178
Dissolved oxygen (*mg/liter*)	499	6.6±1.9	1.1–11.4
Conductivity (*micromhos*)	93	427±49	268–490
Acidity (*mg/liter*)	163	12±3.6	2–21

[a]Mean ± one standard deviation.

were illuminated with white fluorescent lights; the photoperiod followed the natural seasonal variation. Aeration was provided continuously to maintain adequate dissolved oxygen concentrations. Ten 30-cm lengths of 15-cm square flue tiles were placed in each chamber for cover.

Tests were begun in January 1968 and ended in November 1969. Initially 96-hr TL50 values (median tolerance limit) were determined to establish the nominal test concentrations for the other tests. The acute, continuous-flow bioassay water temperature was maintained at 23 C, and duplicate tanks with five fish per tank were used.

For the 20-month exposure experimental fish were collected from a rearing pond at the Newtown Fish Farm and were about 7 months old. Twenty fish were added randomly to each of the nominal test concentrations (4, 8, 16, 32, and 64 μg/liter) and the control. After 20 months the fish were sacrificed, and tissue and blood samples were taken immediately and prepared for eventual analyses as in McKim et al. (1970). The results of analyses of kidney samples from fish exposed to 53 μg/liter in this test were abnormally variable and are not included. Temperatures were recorded continuously and ranged from 5 to 25 C during the 20-month study.

The 30-day test was conducted at the end of the 20-month test, with approximately 2-year-old brown bullheads collected from the same pond from which the initial lot of fish was obtained. The nominal copper concentrations for this test were higher (32, 64, 128, 256, and 512 μg/liter) to provide dead fish for the autopsy study. Dead fish were removed and frozen for future tissue analysis for copper. After 6 and 30 days, live fish were sacrificed and tissue and blood samples were collected as at the end of the 20-month test. Some fish exposed to 32 and 64 μg/liter for 20 days were transferred to 256 and 512 μg/liter to determine the effect of previous sublethal exposure to copper on uptake before death at lethal exposure concentrations. The water temperature ranged between 15 and 20 C.

During most of the tests the fish were fed a mixture of coarsely ground beef heart and pork liver (5:1) and earthworms. They were fed dry fish food and chopped fish during the initial months of the 20-month exposure. No prophylactic treatment was necessary at any time during the tests.

Analytical — Total hardness, *p*H, alkalinity, acidity, conductivity, and dissolved oxygen determinations were made weekly with the procedures described by the American Public Health Association (1965) (Table 1).

Copper was added to the proportional diluters in an aqueous solution of reagent grade $CuSO_4 \cdot 5H_2O$. Analyses for copper in the water were made on either grab samples or samples collected daily and composited for 5 days before analysis. Samples from nominal concentrations exceeding 100 μg/liter were acidified with 3–4 drops of concentrated sulfuric acid per 100 ml, and the copper was measured by atomic adsorption spectrophotometry. Samples with lower nominal copper concentrations were acidified similarly, and aliquots were transferred to tared separatory funnels and weighed. Two milliliters of concentrated nitric acid were added per 100 g and extracted

TABLE 2. Measured total copper concentrations in the test water for the 20-month and 30-day tests.

Nominal concentration (*μg/liter*)	Number of analyses	Mean[a] measured concentration (*μg/liter*)	Range
20-month test[b]			
64	86	53±9.7	42–68
32	83	27±4.9	14–37
16	85	16±2.4	8.5–20
8	83	10±1.9	5.5–14
4	85	6.5±1.8	3.0–9.3
Control	85	3.4±1.2	1.8–5.5
30-day test[c]			
512	7	422	406–439
256	7	206	191–220
128	7	104	97–113
64	6	49	45–55
32	6	27	20–30
Control	3	3.7	3.7–3.8

[a]Mean ± one standard deviation.
[b]All analyses were of composite samples of 5 days each.
[c]Analyses of grab samples and composite samples of 5 days each.

three times with 0.1% diethylammonium diethyldithiocarbamate in chloroform (Stary 1964); the three extractions were shaken for 120, 30, and 30 sec, respectively. The three extracts together with an interfacial cuff from one sample were combined in a beaker to which was added 10 drops of bromine solution. These samples were evaporated to dryness on a hot plate and evaporated to dryness twice more after addition of concentrated nitric acid and 25% concentrated hydrochloric acid. The residue was dissolved in 10% acetic acid, and copper was measured by atomic adsorption spectrophotometry. The mean extraction recovery of 270 spiked samples was 98% with a standard deviation of 5.4%. Reported measured copper concentrations (Table 2) were not corrected for recovery data. Measured copper concentrations in the water will be used in all subsequent discussion.

Tissues were prepared and analyzed for copper by the method of Leonard (1971). All resultant data except those for the blood were based on dry weight.

Results and discussion — The 96-hr TL50 values for 7-month-old brown bullheads were 170 and 190 µg/liter; graphical interpolation was used as described by the American Public Health Association (1965). Acute lethality in the 30-day test was sufficient to calculate a 96-hr TL50 of 186 µg/liter for this second lot of fish. This TL50 value was for 8 fish per concentration at 20 C.

At the lethal and sublethal concentrations of copper tested, there was no accumulation of copper over the control concentration in the opercle, red blood cells, and blood plasma; the means (and ranges) of all values were 3.61 (2.5–10.0), 0.50 (0.35–0.69), and 0.82 (0.56–1.08) µg/g, respectively.

Uptake related to time and concentration was investigated for live fish (Table 3). Equilibrium concentrations of copper in the gill and liver were reached within 30 days. For the water concentrations tested no great difference was apparent in copper concentrations in tissues between the 30-day and 20-month exposures. However, the copper levels in the gill and liver tissues from fish exposed for 20 months

TABLE 3. Copper concentrations (*µg/g dry weight*) in tissues of live brown bullheads (*Ictalurus nebulosus*) after 6-day, 30-day, and 20-month exposures.[a]

Measured copper concentration in water (*µg/liter*)	6 days	30 days	20 months
	Gill		
Control	5.0(2.7–6.2)[b]	5.7(4.6–6.8)	3.8(2.8–5.9)
6.5	– –	– –	4.3(3.5–5.9)
10	– –	– –	4.3(3.8–5.8)
16	– –	– –	3.6(2.4–4.5)
27	9.4(6.8–12)	22(11–28)	6.9(4.8–11)
49–53	12(9.4–15)	26(14–33)	25(20–31)
104	14(8.3–20)	34(19–57)	– –
	Kidney		
Control	7.6(6.2–8.7)	8.0(6.9–9.3)	7.8(5.0–13)
6.5	– –	– –	8.5(6.2–22)
10	– –	– –	8.8(5.2–13)
16	– –	– –	14.3(5.0–51)
27	8.8(6.9–11)	10(6.5–18)	10.0(5.4–18)
49–53	9.0(7.4–11)	13(9.3–20)	– –
104	10(7.0–18)	23(12–45)	– –
	Liver		
Control	24(18–33)	23(13–35)	29(15–37)
6.5	– –	– –	28(11–59)
10	– –	– –	32(16–63)
16	– –	– –	47(28–62)
27	33(18–50)	90(62–143)	61(12–110)
49–53	35(30–56)	112(69–168)	130(100–150)
104	33(24–43)	116(79–181)	– –

[a] $N = 5–8$.
[b] Mean and range.

TABLE 4. Copper concentrations (*μg/g dry weight*) in tissues of brown bullheads (*Ictalurus nebulosus*) killed by exposure to lethal copper concentrations.[a]

Tissue	Copper concentrations in water (*μg/liter*)					
	27–206[b]	49–206[b]	206	27–422[b]	49–422[b]	422
Gill	21(10–46)[c]	24(21–28)	7.7(7.0–9.4)	5.0(17–115)	33(31–36)	13(7.7–17)
Kidney	12(10–14)	12(11–13)	10(7.2–14)	9.2(8.8–9.9)	12(11–12)	8.0(5.2–10)
Liver	48(30–68)	144(110–180)	34(22–54)	75(53–110)	74(63–86)	24(19–27)

[a]N = 2–5. Mortality occurred in less than 4 days.
[b]Fish held for 20 days at 27 and 49 μg/liter before transfer to the lethal concentrations of 206 and 422 μg/liter.
[c]Mean and range.

were relatively constant at the low water concentrations, but at 27–53 μg/liter there was an increase almost as if some "defense mechanism" for copper was being overcome for these tissues. The blood chemistry and physiological changes which occur at this water concentration are discussed by Christensen et al. (1972).

With the exception of those fish transferred from sublethal to lethal conditions, comparison of copper concentrations in the tissues from fish killed by copper (Table 4) with those of live fish exposed for 6 days to lower water concentrations (Table 3) indicates no difference between copper concentrations in the gills, liver, or kidney. As indicated earlier, the concentrations in the opercle were also similar. Tissue concentrations in fish exposed to sublethal water concentrations (27 and 49 μg/liter) before transfer to lethal concentrations were higher than the concentrations in tissues from fish placed directly into the lethal water concentrations. Thus the concentrations of copper in fish killed in natural surface waters would be expected to vary significantly depending upon exposure to sublethal toxicant concentrations before the fish kill. Five live fish were removed from lethal concentrations (207 and 422 μg/liter) after 7 hr of exposure, and the copper concentrations in their tissues approximated those in the tissues of dead fish.

The attempt to develop an autopsy technique for copper similar to that for zinc for five fish species (Mount 1964) and cadmium for bluegills and brown bullheads (Mount and Stephan 1967) indicated that the uptake, distribution, and accumulation of copper in brown bullheads is not similar to zinc and cadmium. These investigators found that gill tissue was the appropriate organ for cadmium, and a ratio of concentrations in the gill and opercle was used for zinc. Their studies also showed a difference between toxicant concentrations in tissues of fish killed by the toxicant and concentrations in tissues of exposed but living fish. Such differences were not demonstrable for copper in the tissues of the brown bullhead. Consequently the use of tissue residues is apparently not an acceptable autopsy procedure for copper.

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Design of a Trapnet with Interchangeable Parts for the Capture of Large and Small Fishes from Varying Depths

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BEAMISH, R. J. 1973. Design of a trapnet with interchangeable parts for the capture of large and small fishes from varying depths. J. Fish. Res. Board Can. 30: 587–590.

The use of new materials and a modification of the basic trapnet design produced nets that fished successfully for large and small fishes in areas where conventional collecting techniques were difficult to apply. Parts of the trap can be interchanged to fish at depths of 1–5 m.

BEAMISH, R. J. 1973. Design of a trapnet with interchangeable parts for the capture of large and small fishes from varying depths. J. Fish. Res. Board Can. 30: 587–590.

Grâce à de nouveaux matériaux et à une modification du plan de base du filet-trappe, nous avons construit des filets capables de capturer de grands et de petits poissons dans des endroits où les agrès de collection conventionnels sont difficiles d'application. Certaines parties du filet-trappe peuvent être interchangées pour pêcher à des profondeurs de 1 à 5 m.

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FISHERIES biologists frequently wish to obtain fishes of all size-classes from habitats that are difficult to sample. If a less abundant species is desired, the use of gillnets or poison usually results in few, if any captures, while destroying many other individuals. Obtaining specimens alive and in good condition also precludes many sampling methods.

In a previous study a modification of conventional trapnet materials and design produced an efficient piece of gear for sampling fishes from shallow-water habitats (Beamish 1972). The 3-ft (90-cm) deep nets were easily set and fished in habitats which, due to the presence of rocks, mud, fallen trees, or such like, were difficult to sample with gear such as seines or gillnets. Their lightweight design made them portable into remote areas. The small-mesh-material made them especially useful for the capture of small fishes. Conventional net-making skills were not necessary and the design could readily be modified to fish in a wide variety of habitats.

The purpose of this note is to describe a new design for a convertible trapnet that is effective in catching small and large fishes in depths ranging from 3 to 15 ft (1 to 5 m).

Materials — Nets are constructed from $\frac{1}{32}$-inch (0.8-mm) square mesh, green mosquito-type, nylon netting. In order to prevent unravelling, only material with threads joined by locking stitches should be used. Samples of the material are available from the author.

A net is cut according to a pattern that efficiently utilizes 3-ft (90-cm) wide material. Seams are double stitched on the inside, single stitched on the outside, allowing a $\frac{1}{2}$-inch (12.5-mm) hem for stringing with $\frac{3}{16}$-inch (4.8-mm) nylon or polypropylene rope. All sewing was done by lightweight sewing machine using medium weight (#36) black nylon thread. The top opening of the crib or pot is fastened with 1-inch (2.5-cm) Velcro®, a nylon hook and loop fastener, which is sewn to the netting along the plain, outside edges. A glue is also available; however, its suitability to extended periods underwater has not yet been determined. Split leads (4–6 oz; 110–170 g) are fastened to the bottom ropes and one-half or short floats are tied to the top ropes (Fig. 1). Short floats are approximately two-thirds the size of floats used on commercial gillnets. Continuous lead and float lines can also be used.

Brails for each wing are made by inserting a piece of 1-inch (2.5-cm) doweling or similar stock into an 8-inch (20-cm) length of 1-inch (2.5-cm) pipe. The bottom, back of the pot is attached to a 48-inch (120-cm) conduit pipe. The top, back of the pot is attached to a 2 × 2 × 48-inch (5 × 5 × 120-cm) piece of cedar. Attachments to pipe and cedar are also by means of snap fasteners in order to allow pots to be interchanged. For a detailed account of the construction of the 3-ft (90-cm) design see Beamish 1972.

Description of net — Designs successfully tested to date include a basic 3-ft (90-cm) design, weight 31 lb (14 kg); the 9-ft (270-cm) net (Fig. 1), weight 48 lb (22 kg), that converts to the basic 3-ft (90-cm) design; and a 6-ft (180-cm) net, weight 35 lb (16 kg), that is similar to the 9-ft (270-cm) model but reduced in proportions and not convertible.

The 9-ft (270-cm) trap differs from the 3-ft (90-cm) trap (Fig. 2) as follows: pot is 5½ ft (165 cm) long; exit of tunnel has a 6-inch (15-cm) square opening; gap is 16 inches (40 cm) wide, i.e. 8 inches (20 cm) on each side of

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the lead; the distance from the gap to the front of the pot is 36½ inches (92 cm); no gap roof; length of inside of heart is 6 ft 1¾ inches (187 cm) and outside of heart is 8 ft 4½ inches (255 cm); wings are 13 ft (4 m) long; the lead is tapered; full size floats are attached at six points where the tapered lead and covering are connnected (Fig. 1). The 9-ft (270-cm) convertible design has a covering extending from the gap, along the 16-ft (490-cm) tapered lead to the inside edge of the heart and onto the posterior 7 ft (210 cm) of each wing (Fig. 1). The taper prevents fishes from passing over the lead and the covering is effectively a tunnel that acts to guide fishes into the heart and thence into the pot. The taper on the lead and the covering are attached by alternating 3 ft (90 cm) of Velcro® with five dome fasteners spaced evenly over 12 inches (30 cm). By removing the taper on the lead and the covering at the positions shown in Fig. 1, the 9-ft (270-cm) design converts to the 3-ft (90-cm) trap, (Fig. 2) and thus can be fished in shallow water. All ropes necessary to string the taper and covering are connected

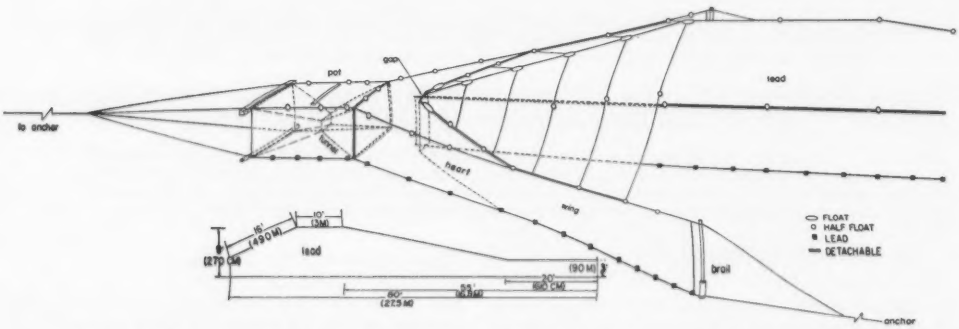

FIG. 1. The convertible 9-ft (270-cm) design showing detachable covering and taper on lead.

TABLE 1. Catch results for the three trapnet designs fished for 4 days at Wolf Lake.[a] (*None captured.)

Fishes reported to be present in Wolf Lake	Trapnet designs set overnight June 2, 1972			Total catch for three trapnets June 2–5, 1972
	3-ft (*90 cm*)	6-ft (*180 cm*)	9-ft (*270 cm*)	
Common shiner *Notropis cornutus*	265	180	350	4050
White sucker *Catostomus commersoni*	270	290	650	2770
Redbreast sunfish *Lepomis auritus*	135	500	2	1490
Brown bullhead *Ictalurus nebulosus*	101	100	61	640
Southern redbelly dace *Phoxinus erythrogaster*	*	2	*	294
Cutlips minnow *Exoglossum maxillingua*	13	5	1	106
Creek chub *Semotilus atromaculatus*	2	5	2	35
Brook trout *Salvelinus fontinalis*	*	*	*	10
Blacknose dace *Rhinichthys atratulus*	1	1	1	5
Slimy sculpin *Cottus cognatus*	*	*	*	*

[a]Wolf Lake has a maximum depth of approximately 45 ft (13.7 m), a surface area of 148 acres (60 ha), and is located approximately 44°02′N, 74°12′W within the Huntington Wildlife Forest near Newcomb, N.Y., U.S.A.

with snap fasteners to the net. A continuous strip of 1-inch (2.5-cm) Velcro® connects the pot to the heart. Thus it is possible to interchange pots of different sizes and with different sizes of tunnel openings.

In general nets received little damage from captured animals capable of tearing the mesh with their teeth or claws. However, on occasion, predators have torn the pot from the outside. To reduce such damage, nets are presently being tested that have an extra thickness of mosquito netting or small-mesh knotless nylon netting attached with dome fasteners to the outside of the pot sides and back.

Netting results—The three designs when fished in Wolf Lake captured nine of the 10 species (Table 1) reported to be present (Dence 1937). Eight species were captured from the first night and more than 9000 fish were captured during a 4-day sampling period. Trapnets of similar design have captured

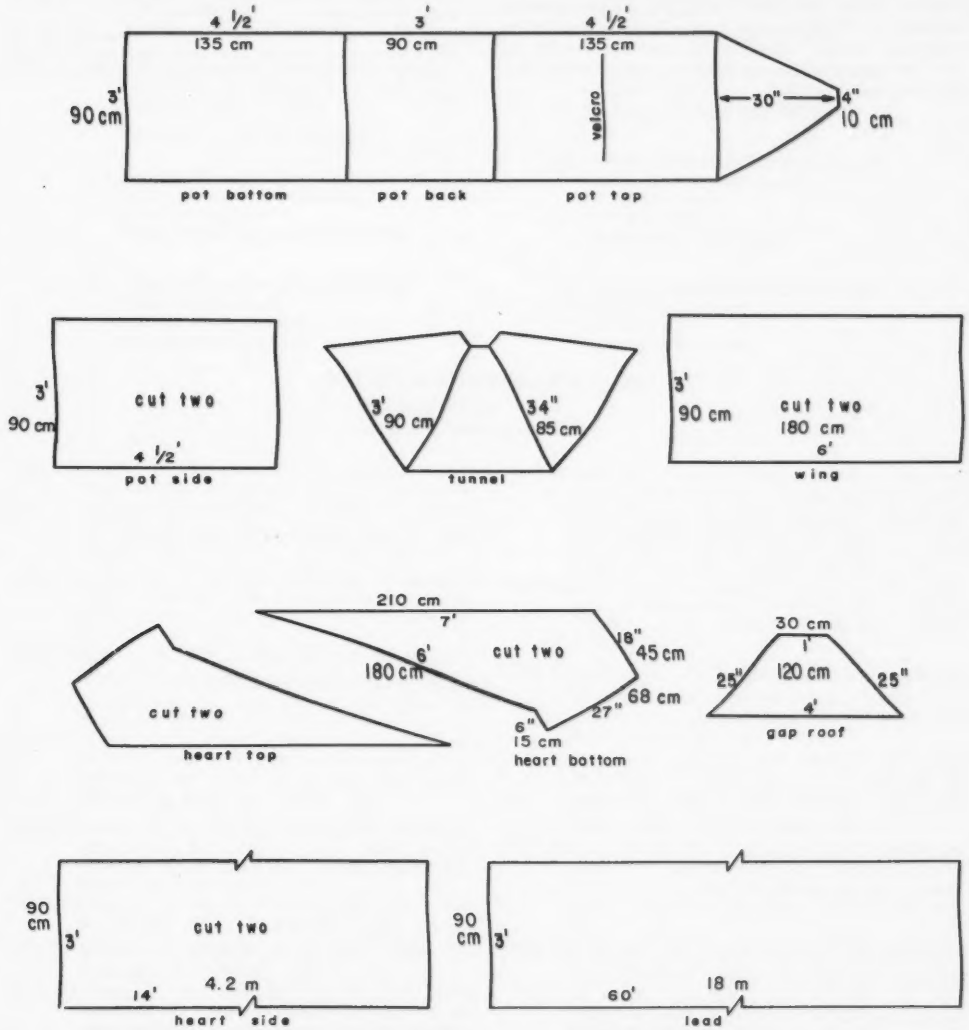

FIG. 2. Net pattern for the 3-ft (90-cm) design.

many other species of small and large freshwater fishes including arctic char (*Salvelinus alpinus*), lake whitefish (*Coregonus clupeaformis*), rainbow trout (*Salmo gairdneri*), smallmouth bass (*Micropterus dolomieui*), northern pike (*Esox lucius*), walleye (*Stizostedion vitreum vitreum*), and yellow perch (*Perca flavescens*). They have also fished successfully in some marine habitats. Nets have not fished well in waters where strong currents existed. Dimensions of the lead quoted in this report were designed to produce traps that would conform to the general bathymetry of lakes under study. Persons wishing to construct similar traps should consider modifying the lead dimensions according to the particular habitats being studied.

Acknowledgments — The various designs tested were sewn by A. Beamish. The author appreciates the comments of Dr H. H. Harvey, Mr B. W. Fallis, Mr S. N. Tibbo, Dr W. B. Scott, and those people who have constructed trapnets of similar design and reported on their catches.

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Recent Articles on FRB Investigations Published in Other Periodicals

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles, which henceforth may be obtained in reprint form only from the author or originating FRB establishment. The number following each title refers to the FRB establishment listed below.

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(August 22–29, 1974)

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